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THE UNIVERSITY OF ALBERTA

NATAL DISPERSAL IN COLUMBIAN GROUND SQUIRRELS

BY

DARWIN R. WIGGETT

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

ZOOLOGY

EDMONTON, ALBERTA
SPRING 1988

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled NATAL DISPERSAL IN COLUMBIAN GROUND SQUIRRELS submitted by DARWIN R. WIGGETT in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

DA Boag

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Date Nov 23/87

Abstract

Dispersal of yearling Columbian ground squirrels (*Spermophilus columbianus*) was studied at three small isolated colonies in the Sheep River-Gorge Creek drainage of southwestern Alberta during 1984-1986. The purpose of this study was three-fold: 1), to provide a description of dispersal within and between isolated colonies for comparison with the descriptive work of others who have studied ground squirrel dispersal in areas of continuous habitat; 2), to test the hypothesis that dispersal is initiated when a critical threshold in weight is acheived; 3), to test the alternative hypothesis that dispersal is prompted by aggressive interactions with conspecifics.

Individuals that dispersed (permanently departed from their natal home range and former neighbours) either dispersed within colonies (intracolony dipersers) or departed from the natal colony (intercolony dispersers). For yearlings 73% and 16% of males and 26% and 5% of females were intercolony and intracolony dispersers respectively. Intercolony dispersal appeared to incur costs both in terms of survival and body condition (weight loss) whereas intracolony dispersal did not appear to involve such costs.

Dispersal did not appear to be initiated when a critical weight was reached. Instead a critical weight appeared to be a necessary prerequisite to dispersal. Individuals that did not achieve a minimum critical weight by the time that most dispersal was occurring apparently delayed dispersal until the following season.

Kinship, demographic, and behavioural parameters were all shown to correlate with dispersal. All correlates suggested that dispersal was proximally initiated by conspecific agonism. For males, the frequency and rate of agonistic interaction with yearlings of both sexes (but particularily with other yearling males) and with adults (both male and female) were correlated with their dispersal history while for females ~~the rate~~ and frequency of agonistic interactions with close female kin (mother and sisters) and unrelated adult females seemed to be the most important determinants of dispersal.

In comparing the results of this study with those of other ground squirrel studies, it became apparent that the differences between studies, in terms of the proximal causes of dispersal, were explained by differences in social structure and habitat. I discuss the evolution of male-biased natal dispersal in the Columbian ground squirrel in light of these observed differences.

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Without the help and advice of all those listed below this thesis would not exist as presented here. Each provided positive contributions to the development of this work. Any omissions, errors, or misinterpretations within this thesis are solely my responsibility and not the responsibility of those acknowledged.

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I. General Introduction

The genetic and demographic consequences of dispersal are well known; dispersal can have a significant impact on the size, composition, regulation, longevity, genetic structure, and social organization of populations (Howard 1949, MacArthur and Wilson 1967, Hamilton 1972, Roff 1974, Lidicker 1975, Hedrick *et al.* 1976, Endler 1977, Tamarin 1978, Sheilds 1982, Moore and Ali 1984). Although dispersal has been documented in a wide variety of vertebrates (see reviews by Lidicker 1975, Gaines and McClenaghan 1980, Greenwood 1980, Dobson 1982, Greenwood and Harvey 1982, Waser and Jones 1983, Holekamp 1984a, Pusey and Packer 1987) relatively little is known about the immediate (proximate) and evolutionary (ultimate) causes of dispersal (see references cited above).

Greenwood (1980) classified dispersal into two categories; **breeding dispersal** , the movement of reproductive adults between successive breeding sites and **natal dispersal** , the movement of prereproductive young from their birth place. Natal dispersal is much more common and widespread than breeding dispersal (Baker 1978, Greenwood 1980, Dobson 1982) and recently has been the focus of much empirical and theoretical study. Natal dispersal is decidedly sex-biased; among birds females usually disperse (Greenwood 1980, Greenwood and Harvey 1982), whereas among mammals males usually disperse (Gaines and McClenaghan 1980, Greenwood 1980, Dobson 1982, Holekamp 1984a, Pusey and Packer 1987).

A sex-bias in dispersal along with other lines of evidence have led many to speculate that dispersal evolved as a mechanism to prevent close inbreeding (Dobson 1979, Packer 1979, Dobson 1982, Cockburn *et al.* 1985, Holekamp 1986). Others have argued that dispersal has evolved as a result of competition for mates (Dobson 1982, Moore and Ali 1984) or essential resources (Lidicker 1975, Boutin *et al.* 1985, Waser 1985). Some researchers have tried to test ultimate hypotheses of dispersal through direct experimentation (eg. Dobson 1979). Such experimentation assumes a direct link between proximate mechanisms and ultimate causation. In other words, "whether evolutionary mechanisms thought to operate over thousands of generations can be expected to respond to manipulations within the confines of a short term experiment remains to be determined" (Hackett 1987, p. 3). I concur with Holekamp (1983) and Hackett (1987) that progress in the understanding of the adaptive significance of dispersal will come first through detailed studies of causation at the proximate level followed by later extrapolation to the ultimate level. In this thesis I attempt to elucidate the proximate causative factors of natal dispersal in the Columbian ground squirrel (*Spermophilus columbianus*).

Holekamp (1984a), in reviewing ground squirrel dispersal, rejected conspecific aggression as a probable cause of dispersal among young males (the predominant dispersing sex). Most ground squirrels of the genus *Spermophilus* disperse during their first active season as juveniles, but *S. columbianus* is an exception; most dispersal occurs during the second active season at 1 year of age (Boag and Murie 1981, Festa-Bianchet and King 1984, Holekamp 1984a, Hackett 1987). Among most species of *Spermophilus*, levels of aggressivity are high during the breeding season as well as later during gestation and lactation (Michener 1983, 1984, McLean 1984). After juvenile emergence, aggression drops to low levels and adults (especially males) may begin preparing for and entering hibernation (Michener 1983, Holekamp 1984a, McLean 1984, Michener 1984). Thus juvenile dispersal in most ground squirrels occurs during periods of low aggression when adults may be entering hibernation; whereas dispersal of yearling Columbian ground squirrels coincides with lactation and juvenile emergence, a period when highly aggressive interactions occur (Festa-Bianchet and King 1984, Hackett 1987). It is conceivable, then, that conspecific aggression causes yearling dispersal. In fact, two studies on the behaviour and dispersal of Columbian ground squirrels (Festa-Bianchet and King 1984, Hackett 1987) have suggested that conspecific aggression may initiate natal dispersal.

Holekamp (1983, 1984a,b, 1986) has argued that social interactions do not appear to cause dispersal in male ground squirrels. Based mostly on her work with Belding's ground squirrels, *S. beldingi*, Holekamp has hypothesized that natal dispersal in male ground squirrels may be triggered by the attainment of a critical weight threshold which in turn triggers an "ontogenetic switch" in development which initiates dispersal. Thus, according to Holekamp, the timing of dispersal should correlate directly with body weight. In this thesis I address two possibilities; one, that dispersal of yearling Columbian ground squirrels is caused by acheivement of a critical weight threshold as described by the "ontogenetic switch" hypothesis of Holekamp (1983, 1984a,b, 1986), or two, that dispersal is the result of conspecific aggression as hypothesized by Festa-Bianchet and King (1984) and Hackett (1987).

This thesis is divided into five main chapters plus a general introduction and conclusion. I examine correlates of body weight and dispersal in Chapter 5 in order to test the "ontogenetic switch" hypothesis. I examine dispersal in relation to spatial and social organization (Chapter 3), social behaviour (Chapter 4) and kinship and demography (Chapter 6) in an attempt to test the conspecific aggression hypothesis. In addition, I provide a description of dispersal of Columbian ground squirrels from small isolated populations (Chapter 2) as a contrast ~~to~~ Hackett's description of dispersal within a large more continuous population. The influence of habitat structure (isolated versus continuous) on ground squirrel dispersal is a secondary theme of this thesis. As well, I discuss my results in light of current evolutionary theory and speculate on the evolution of yearling dispersal in the Columbian ground squirrel.

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II. Intercolony Natal Dispersal in the Columbian Ground Squirrel

Introduction

"Natal" dispersal is the movement of prereproductive individuals from their place of birth (natal home range) to a new home range elsewhere where they may attempt to breed (Lidicker 1975, Greenwood 1980, Holekamp 1984a). Among members of the social ground-dwelling sciurids as in most other species of polygynous mammals, natal dispersal is decidedly sex-biased with more males than females dispersing or with males moving farther than females (Greenwood 1980, Armitage 1981, Dobson 1982, Michener 1983, Holekamp 1984a). Documentation of natal dispersal has relied mostly on inference rather than direct evidence. For instance, in many ground squirrel studies, disappearance rates of young animals (mostly male) over the active season have been attributed to dispersal because: 1) the loss is synchronous and predictable (that is, the disappearance of animals occurs over a relatively short period at a predictable time in the annual cycle and this pattern of loss is relatively constant within a species - see Holekamp 1984a for review), 2) before disappearing, individuals in this cohort increase their range of movements, and make frequent excursions from their natal home range (Quanstrom 1971, Slade and Balph 1974, Dunford 1977, Davis 1982, Holekamp 1984a, Hackett 1987), 3) during the disappearance phase unmarked or marked animals from elsewhere appear for the first time on the study area - these animals are known or presumed immigrants (Dunford 1977, Dobson 1979, Festa-Bianchet and King 1984, Holekamp 1986, Wiggett and Boag 1986), and 4) a small proportion of disappearing marked animals are sighted or recaptured at considerable distances from the study site (Quanstrom 1971, Svendson 1973, Boag and Murie 1981a, McLean 1982, Holekamp 1983, Festa-Bianchet and King 1984, Sherman and Morton 1984, Knowles 1985, Wiggett and Boag 1986).

Recent developments in radio-telemetry have enabled researchers to relocate these disappearing animals, follow their movements, and determine their fates (Holekamp 1983, 1984b, 1986, Hackett 1987, Garrett and Franklin in press). These studies confirm that disappearing animals were indeed dispersing. Such studies also provide useful information on how far animals move before settling. For example, Hackett (1987) documented dispersal distances of 62 to 980 m for yearling Columbian ground squirrels (*Spermophilus columbianus*) that lived in an area of continuous habitat. By contrast, Festa-Bianchet and King (1984) recorded dispersal distances of 2 to 3 km for yearling *S. columbianus* that resided in a small (1.06 ha) isolated meadow. Boag and Murie (1981) and Wiggett and Boag (1986) recorded dispersal movements of up to 6.5 and 1.7 km respectively for yearling *S. columbianus*. Obviously these ground squirrels are capable of long distance dispersal. Hackett (1987) found that dispersing animals settled where vacancies (unused burrow systems) existed and that the distribution of dispersal distances reflected the distribution and availability of vacant burrow systems. Thus, animals living in large areas of continuous habitat may only have to disperse relatively short distances to find suitable vacancies (eg. in Hackett's 1987 study), whereas animals living in small isolated meadows (such as that described by Festa-Bianchet and King 1984) may have to travel great distances to find suitable vacancies in appropriate habitat.

Long distance dispersal between isolated patches of habitat poses additional difficulties to those encountered by animals that disperse across areas of continuous habitat. For instance, how do interpatch dispersers find their way to other areas of suitable habitat and how dangerous are such movements? These are questions that few studies address because of the difficulties inherent in obtaining such data. Nevertheless, such information is critical to understanding the ecological and evolutionary consequences of dispersal. The purpose of this chapter is to document in greater detail the occurrence of intercolony dispersal in *S. columbianus*, and to compare intracolony dispersal in continuous habitat (as in Hackett 1987 and Chapter 3) with intercolony dispersal between isolated patches of habitat in terms of timing, manner of movement, and success rate in transit.

Methods

Definitions

Colony: a discrete meadow area containing ground squirrel burrow systems in active use. All colonies (meadows) studied were separated from other colonies by areas of unsuitable ground squirrel habitat such as forest, bog, or talus.

Intercolony dispersal: any one-way movement of an individual animal between two or more colonies.

Intracolony dispersal: any movement of an individual animal within a colony that results in a complete and permanent shift in home range *and* spatial associates (neighbours). Operationally, any permanent shift in home range that results in an animal living greater than or equal to 2 adult-sized home ranges away from the original natal home area--see Chapter 3 for further details and discussion.

Continuous habitat: any habitat containing essential resources (eg. food, burrow systems, hibernacula, etc.) that is physically large enough to enable any individual in the population to undergo an intracolony dispersal movement in at least two directions - operationally any colony with a physical area $\geq$ 2.4 ha (see Appendix 1 for details and discussion).

Discontinuous (patchy) habitat: any area of suitable habitat that is physically too small to allow every individual in the population the possibility of making an intracolony dispersal movement in at least two directions - any area $\leq$ 2.4 ha in size.

General methods and study areas

Demographic attributes of 16 different colonies of Columbian ground squirrels were recorded for varying periods of time between 1973 and 1986 in the Sheep River-Gorge Creek drainage system of southwestern Alberta (Table 2.1 and Fig. 2.1). Boag and Murie (1981a) provided a general description of the area. The 16 colonies studied total 91 colony years of

Table 2.1 Details of 16 colonies of Columbian ground squirrels in the Sheep River-Gorge Creek drainage of southwestern Alberta (see Figure 1 for locations).

Colony (abbreviation)	Years studied	Intensity of study[1]	Size of meadow (area occupied by squirrels)	Habitat classification[2]	Elevation in meters	$\bar{X}$ size of spring population (range)
Windy Point (WP)	1973-1979	3	>5 ha	C	1400 m	150[3]
Hay Meadow (HM)	1973-1979	2	72 ha	C	1450 m	750[3]
	1985-1986	3				
Gorge Creek (GC)	1979-1982	3	1.2 ha	D	1400 m	
	1983-1986	2				19 (13-26)
North Fork East (NFE)	1982-1983	2	2.5 ha (1.3 ha)	D	1590 m	18 (13-23)
	1984-1986	1				56 (39-71)
North Fork West (NFW)	1983	2	5.1 ha (3.47 ha)	C	1580 m	
	1984-1986	1				77 (65-94)
Artificial A (AA)	1983-1986	1	3.98 ha (1.9 ha)	D	1500 m	13 (3-27)
Artificial B (AB)	1983-1986	1	2.39 ha (0.34 ha)	D	1500 m	7 (2-14)
Dyson Creek (DC)	1979-1986	1	1.06 ha (1.06 ha)	D	1570 m	48 (26-72)
Rosengroen (RG)	1979-1980	2	1.62 ha (1.27 ha)	D	1630 m	19 (15-22)
	1981-1982	3				>12
	1983	2				18
	1984-1986	1				33 (24-46)
Mt. Hoffman (MH)	1982/1986	3	>5 ha	C	1750 m	>50
Indian Oils (IO)	1973-1981	3	1.3 ha	D	1550 m	25[3]
	1982-1986	2				22 (20-26)
Blue Rock (BR)	1982	3	1.5 ha	D	1600 m	>25
	1983-1986	2				26 (22-29)
Sheep River (SR)	1982	3	>3 ha	D	1600 m	50
McLean's Mill (MM)	1982-1986	2	0.9 ha	D	1650 m	8 (7-9)
Junction Creek (JC)	1982	3	1.1 ha	D	1590 m	>8
	1983-1986	2				15 (9-19)
Sawdust Pile (SP)	1985/1986	3	0.6 ha	D	1660 m	10

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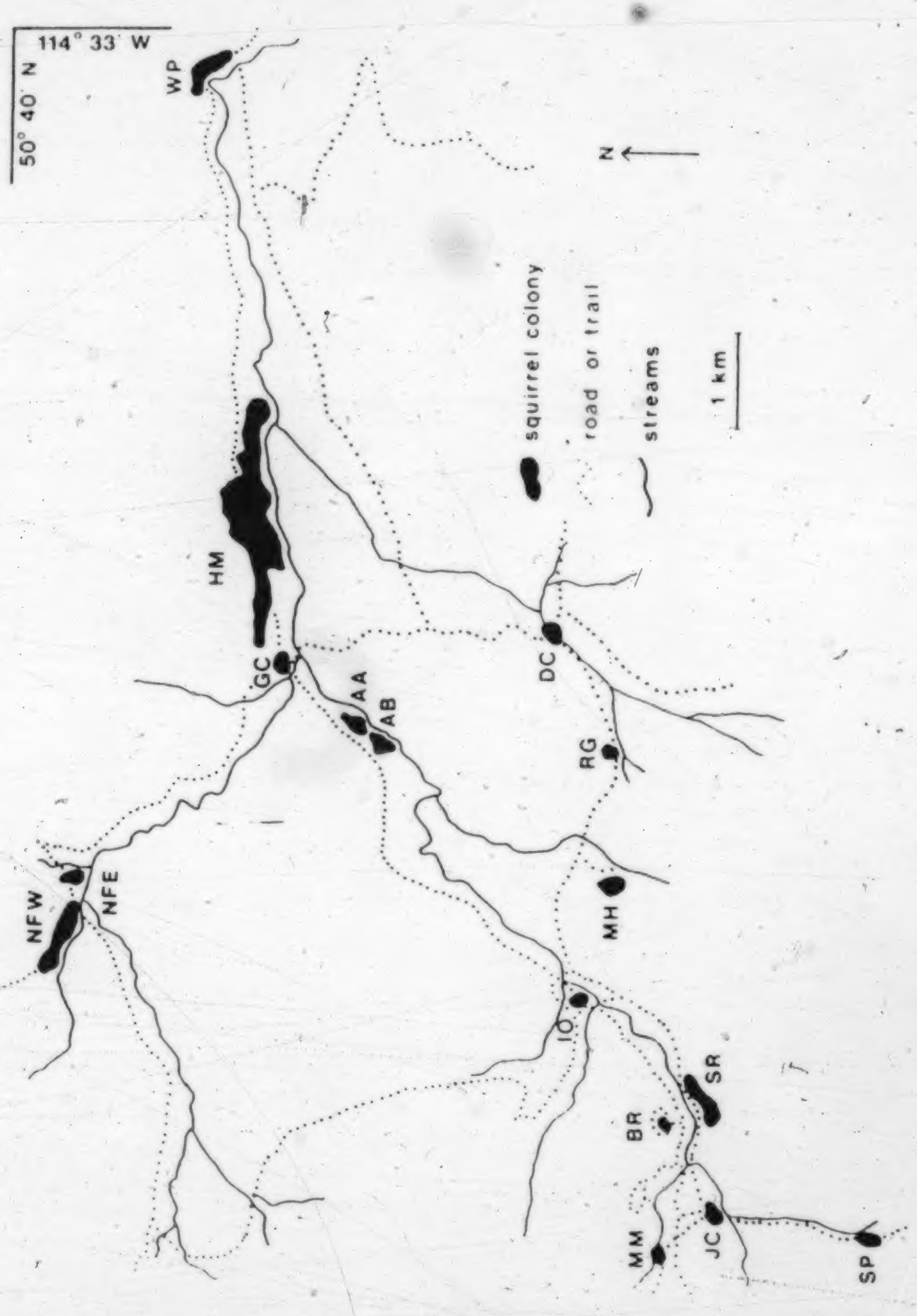
[1] 1 = behavioural and demographic data collected, 2 = demographic data only, 3 = incomplete or ephemeral collection of demographic data (see Methods for more details).

[2] C = continuous, D = discontinuous

[3] See Boag and Murie (1981a) for details

Fig. 2.1. Location of 16 Columbian ground squirrel colonies studied in the Sheep River-Gorge Creek drainage of southwestern Alberta.


114° 33' W
50° 40' N
WP
HM
GC
AA
AB
DC
RG
NFW
NFE
MH
IO
SR
BR
MM
JC
SP
N
squirrel colony
road or trail
streams
1 km

data. The data for each colony-year were placed in one of three categories based on intensity of study.

Category 1 colonies (hereafter C1 colonies): These colonies (six in total - Table 2.1) were studied intensively and provide a total of 25 colony-years of data. Virtually every individual residing in a C1 colony was livetrapped using National live traps (15 x 15 x 50 cm) baited with peanut butter. Upon capture each animal was individually marked with a numbered fingerling fish tag (Monel #1) in each ear and each animal was marked with a unique dye symbol by applying hairdye (Lady Clairol Blue-Black #124) to each animal's pelage with a narrow paintbrush. At each capture the date, tag number(s), dye mark, sex, age, reproductive condition, weight, and location were recorded. At regular intervals, approximately every 10-14 days, an attempt was made to recapture all animals residing in C1 colonies. Trapping success varied but usually 80 to 100% of all animals present were captured during each trapping rotation. Every individual in a colony was captured at least once a season and approximately 90% were captured and handled a number of times over a season. Unmarked squirrels were categorized as juveniles, yearlings, or adults, based on weight, reproductive status, and time of year (Boag and Murie 1981b). Reproductive status was based on condition of genitalia and mammae (Murie *et al.* 1980). Weight was measured to the nearest 10 g using spring scales (Model: Big Jim - 1500 g). Location of capture within a colony was obtained from the coordinates of a grid system established at each colony at the initiation of the study. Fluorescent coloured plastic flags on wires were used to delineate grid corners of each 10 x 10 m grid square. Yearling and adult animals were classed as residents if they emerged from hibernation in the spring and remained present until the end of the breeding season (Murie and Harris 1978, 1984). Juveniles were classed as resident if they were born in the colony in which they lived. No juveniles lived outside their natal colony. Any unmarked non-juvenile or any animal previously marked at a different colony that appeared on a study site during the active season was classed as an immigrant. Animals residing in their natal colony were called natal residents, whereas animals that were residents of a colony but were not born there were referred to as immigrant residents.

Observation platforms were used in each C1 colony (except AA and AB from 1983 to 1985) from which animals in each colony were observed intensively (see Festa-Bianchet 1982, King 1984, and Chapter 4 for details). These observations provided details on behaviour patterns, social interactions, and space use for individual animals which are summarized elsewhere (Festa-Bianchet 1981, Festa-Bianchet 1982, Festa-Bianchet and Boag 1982, Festa-Bianchet and King 1984, King 1984, King and Murie 1985, and Chapters 3, 5, and 6).

Finally, matrilineal relationships for nearly all animals born on these study areas were determined based on patterns of maternal defense of nest burrows and behavioural association of mother and newly emerged offspring (Festa-Bianchet 1982, King 1984, Waterman 1985 1986, Hackett 1987). Thus for C1 colonies, detailed information on individual past history (age, sex, maternal geneology, reproductive history, behaviour, and space use) existed as well as information on general demography.

Category 2 colonies (C2 colonies): These colonies were studied less intensively than C1 colonies and comprise 35 colony-years of data (Table 2.1). No behavioural studies were done in these colonies; therefore no detailed life histories are known for any individual save for what can be inferred from trapping data. The animals in category 2 colonies were marked and released using live-traps as previously described for C1 colonies except that the trap rotation was slightly longer; 10 to 20 days, and trapping success between rounds was lower, 60-100%. Somewhat fewer (80 to 100%) animals residing in C2 colonies were captured each season, so the demographic data are not as complete as in C1 colonies.

Category 3 colonies (C3 colonies): For the most part the colonies listed in Table 2.1 as C3 colonies were trapped neither sufficiently nor regularly enough to have confidence in any demographic data. These ephemerally trapped colonies are of interest only because there has been exchange of marked animals between these and colonies studied more intensively.

Documentation of intercolony dispersal

Positive confirmation of intercolony movements was attainable only when previously marked animals from one colony were recaptured or resighted in a colony elsewhere. Such animals were categorized as known intercolony dispersers.

Animals that disappeared from their natal colony during the synchronous and predictable dispersal period (Boag and Murie 1981a, Festa-Bianchet and King 1984, Hackett 1987) but that were never subsequently recaptured were classed as presumed intercolony dispersers. Presumed dispersers were not recaptured or resighted if they either dispersed to unstudied populations elsewhere or died in transit. A large number of unstudied ground squirrel populations exist in and around those studied, and each year numbers of unmarked animals immigrated into the studied populations, presumably from colonies where squirrels were not marked. I assume, therefore, that a substantial number of marked animals emigrated to unstudied populations, never to be recaptured or resighted, thus limiting the total number of *known* intercolony dispersers. The number of marked animals emigrating to unmarked populations could be estimated from the proportion of marked to unmarked immigrants entering the studied populations (C1 and C2 colonies). This estimate assumes an exchange of animals that is proportionally equal between studied and unstudied populations. Estimates of survival in transit were calculated based on the average ratio of natal versus immigrant 2-year-old residents present in C1 and C2 colonies (details of the calculation are given in the Results-Discussion section).

Disappearance during the dispersal period could result not only from emigration from the study site but also from undetected sources of mortality on site prior to dispersal (eg. predation during excursions - Holekamp 1984a, b). Thus, disappearance rates probably overestimate dispersal. Hackett's (1987) work on dispersal of Columbian ground squirrels in continuous habitat showed that mortality during excursionary movements and dispersal movements in yearling males and females was nil and that actual dispersal rate and estimated dispersal rate based on disappearance did not differ significantly. Therefore I assume the predictable and synchronous disappearance of animals from the study colonies to be dispersal from the site and not a result of undetected mortality on site during that time. All known mortality (predation, disease, trap death, etc.) *plus* all assumed mortality (disappearance outside of the dispersal period) in all age and sex classes except juveniles usually accounted for a loss of only about 5% during the active season in C1 colonies (unpubl. data and Table 2.2). Therefore, since excursions on site do not appear dangerous (Hackett 1987), and since rates of mortality (known *and* assumed) are very low outside the dispersal period, I assume that mortality rates on site during dispersal were also low and similar to those recorded outside the dispersal period. All yearlings that disappeared during the dispersal period were classed as presumed intercolony dispersers. No correction was made for on site mortality during dispersal since such mortality was assumed to be insignificant (~5%).

I use disappearance during the dispersal period to calculate rates of dispersal from a colony (emigration) as follows: emigration rate equals the total number of known intercolony emigrants plus the total number of presumed emigrants divided by the total number of animals known to be alive within 10 days (= 1 trap rotation) of the beginning of the dispersal period. Immigration rate equals the total number of marked and unmarked immigrants divided by the total number of adults and yearlings of the same sex present after the dispersal period is over. Immigration and emigration rates were calculated only for C1 and C2 colonies.

No animals were radiocollared in this study, hence it was not possible to follow individuals during intercolony dispersal movements. It is not known how dispersal movements were accomplished. I developed a random-linear movement (RLM) model to test the idea that animals might be dispersing from colonies in random directions along relatively straight line courses. Under the constraints of this model, I assumed that dispersers would continue along such a course until a new colony was found or until they died in transit (predation, starvation, etc.). Since so few animals dispersed more than 4 km (see Results-Discussion), I assumed that the probability of an animal travelling to encounter colonies greater than 4 km

Table 2.2 Disappearance of yearling male and female Columbian ground squirrels over the active season in Category 1 colonies (n = 20 colony years).

	Total number of yearlings that emerged in spring	Number (%) disappearing before dispersal period	Number (%) disappearing during dispersal period[1]	Number (%) disappearing after dispersal period	Total % loss over active season
Male	220	8 (4)	158 (72)	1 (1)	76
Female	168	12 (7)	45 (27)	1 (1)	35

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[1] Dispersal period = the maximum calendar date extremes of known intercolony exchanges of yearling males and females (4 June to 15 July - see Fig. 2.3)

distant was low and thus I did not incorporate such long-distance movements into the model. An expected number of intercolony exchanges for colony pairs less than or equal to 4 km distant could be calculated as the degree angle ratio (the degree width of the receiving colony divided by 360 degrees) multiplied by the total number of yearlings disappearing from the source colony during the time when both colonies were simultaneously intensively studied (C1 and C2 colonies only). This expected number could then be compared with the observed number of exchanges between colony pairs to test for differences.

All dispersal distances reported are straight-line measurements from maps or aerial photos with no corrections made for topography. Statistical procedures followed are those outlined by Sokal and Rohlf (1981) and Zar (1981). Differences between sets of data were considered significant when $P<0.05$. Parametric statistics were used if the data approximated a normal distribution; otherwise nonparametric statistical inference was applied.

Results and discussion

Who dispersed?

A total of 73 intercolony dispersal movements involving 66 different animals were recorded among colonies between 1973 and 1986 (Table 2.3). Yearlings accounted for 84% of all intercolony movements; adults accounted for the remaining 16%. No juveniles were recorded moving between colonies. If intercolony dispersal were independent of age class (excluding juveniles) then the proportions of all animals undertaking intercolony dispersal movements should be 44% yearlings and 55% adults (based on the average ratio of yearlings to adults in C1 and C2 colonies, n = 1435 squirrels in 60 colony-years). The observed ratio of 84% yearlings and 16% adults differed significantly from expected (X^2 = 48.65; $P<0.001$) indicating that yearlings are more likely than adults to disperse to a different colony.

The number of intercolony movements of adults recorded in this study was probably much higher than normal as a number of these dispersals were induced by human

Table 2.3 Summary of the number of intercolony dispersal movements by age and sex for Columbian ground squirrels in all colonies (C1, 2, and 3) in the Sheep River-Gorge Creek drainage. Numbers in parentheses are number of animals.

	Adults (2+)	2-year-old	Yearlings
Male	7 (3)	3 (2)	48 (48)
Female	2 (2)	0	13 (11)

intervention. For example, of the two adult females that dispersed between colonies (Table 2.2), one animal dispersed from its natal colony, DC, to GC (distance 2.8 km) as a three-year-old after its home area had been disturbed by a bulldozer prior to its emergence from hibernation. This animal left approximately 3-4 weeks after its emergence from hibernation possibly because it could not acquire a new territory at DC where ground squirrel densities were unusually high (Festa-Bianchet and King 1984). The other female (a 4-year-old) was removed from its natal colony (NFW) and taken 4.3 km to a distant colony (HM) where it was released on 27 April, 1986. This female was subsequently sighted and recaptured on AA, 13 July, 1986 (distance moved 2.2 km). Similarly, one adult male that had dispersed from NFW to NFE as a yearling in 1984 was transferred back to NFW on 17 April, 1986; 5 days later it moved back to NFE (distance 0.8 km) to reoccupy its former territory. These two animals were transferred into new colonies at the peak of territoriality among breeding adult males (Murie and Harris 1978) and thus may have been forced out of the colonies into which they were transferred by the territorial residents.

An adult male that had dispersed as a yearling from DC to NFW in 1980 was later transferred to AB in 1983 as part of a colony establishment experiment (Wiggett and Boag 1986). Subsequent to its release on AB, it moved to AA in late June, 1983 where it resided until late June, 1985. Sometime between 22 June and 6 July it returned to AB. In mid April, 1986, it emerged from hibernation in AB but sometime before 2 May had moved to AA only to return to AB shortly thereafter (between 2 May and 5 May) where it remained until immergence.

Another male also moved regularly between AA and AB. This male immigrated onto AB from HM in 1983 as a yearling (Wiggett and Boag 1986). In 1985, when it was 3 years old, it moved from AB to AA between 1 May and 7 May only to return sometime after 12 June. AA and AB are separated by a 160 m wide forested ravine but only a small portion of each meadow is occupied by squirrels (Table 2.1). Thus, both adult males had to move across the ravine and over the unoccupied portions of the two meadows each trip, a distance of about 350 m.

The causes of these movements of the two adult males between AA and AB are not known but anecdotal evidence suggests that avoidance of high social aggression (in 2 cases) and searching for sexually receptive females (in 3 cases) may have prompted these movements. Both animals dispersed from AA in late June, 1985. During this time AA was occupied by five resident adult males, one resident yearling male, and five immigrant yearling males. Immigrant males are often subject to high levels of aggression particularly from resident adult males (D. Wiggett, unpubl. data). Adult male aggression is high in June and female agression peaks with juvenile emergence in June (Chapter 6). The relatively large number of males combined with maternal aggressiveness of 7 females with litters may have prompted the two adult males (both aware of the existence of AB) to disperse there in order to avoid potentially high levels of aggressiveness at AA. At the time of their arrival at AB only three males (one adult, two yearlings) and two reproductively active females were present. Thus the level of aggression at AB was probably much lower than at AA. The other three movements of these two adult males occurred during the breeding season and may have been searches for sexually receptive females. In support of this suggestion is the observation of Murie and Harris (1984) that adult home range shifts in Columbian ground squirrels resulted in males increasing their proximity to females.

The final three intercolony dispersal movements recorded for adults were undertaken by two 2-year-old males. One male dispersed from its natal colony (SR) in 1982 sometime after 17 June; it was later recaptured at MM on 25 June (distance = 1.2 km) and still later at JC (distance = 0.75 km) on 13 July. The other male left its natal colony (BR) after 29 May 1986 and was recaptured at JC on 16 July 1986 (distance = 1.1 km). Both animals were sexually immature and light in weight for their age, and were considered to be delayed natal dispersers (see Chapter 5 for details).

Thus of the 12 intercolony dispersal movements recorded for adults (Table 2.3), only the three moves by the two small 2-year-olds probably represent "natural" dispersal movements. The other 9 intercolony exchanges involving adults were likely artifacts of unusual circumstances; eg. transfers (three cases), habitat loss (one case), and the existence of a nearby, familiar and easily accessible neighbour colony (five cases).

Of the 64 "natural" dispersal movements recorded, 61 (95%) involved yearling-aged animals and only 3 (5%) involved adult-aged animals, the 2-year-olds, which were sexually immature. Such an age bias in dispersal (and presumed dispersal) is consistent with the results of previous research on Columbian ground squirrels. In southwestern Alberta, Boag and Murie (1981a), Festa-Bianchet and King (1984), Murie and Harris (1984), Dobson and Kjelgaard (1985), Wiggett and Boag (1986), and Hackett (1987) all found yearlings to be the predominant disappearing and/or dispersing age class. In Washington *S. columbianus* may disperse as juveniles possibly because the longer active season permits them to disperse and still gain sufficient weight to survive hibernation (Hackett 1987). In southwestern Alberta no dispersal (either inter- or intracolony) of juveniles has been reported (see citations above) except for Dobson and Kjelgaard (1985) who noted immigration of unmarked juveniles onto food supplemented study sites. The distance traveled from the natal home range by these "immigrant" juveniles was not known. Moreover such immigration was likely an artifact of the food supplementation and occurred on continuous habitat.

Boag and Murie (1981a), Festa-Bianchet and King (1984), and Hackett (1987) documented dispersal (both inter- and intracolony) of small numbers of adults. Most of these animals were 2-year-old males and were considered delayed natal dispersers (Chapter 5). Festa-Bianchet and Boag (1982) and Murie and Harris (1984) reported that most adult *S. columbianus* are relatively sedentary and show strong site fidelity over time. This contention is supported by the findings presented here (strong fidelity to a colony) and in Chapter 3 (strong fidelity to a home area within a colony). Thus, in summary, in southwestern Alberta juvenile *S. columbianus* probably never, adults rarely, and yearlings often undergo intercolony dispersal.

In addition to the observed age-bias, intercolony dispersal movements were strongly sex-biased (Table 2.3). Known intercolony dispersal of male and female yearlings (4.4 males: 1 female, Table 2.3) was significantly different from expected($X^2 = 17.97$, $P<0.001$) had dispersal been independent of sex (average yearling sex ratio: 1.2 males: 1 female $n = 618$ squirrels in 60 colony years), with many more yearling males moving than yearling females.

Of 338 males captured and marked as juveniles and present as yearlings in C1 and C2 colonies, 40 were known and 210 were presumed intercolony dispersers. This represents a 74% loss of yearling males from their natal meadows. Among yearling females this loss was only 27% (8 known dispersers and 67 presumed dispersers of 280 animals present). Again, males had a significantly greater tendency to disperse from the natal colony than did females ($X^2 = 236.12$; $P<0.001$). Recovery rates of intercolony dispersers were not significantly different for male and female yearlings; 40 (16.0%) of 250 presumed male dispersers and 8 (10.6%) of 75 presumed female dispersers were subsequently recaptured elsewhere ($X^2 = 0.90$; $0.75>P>0.50$).

A male bias in dispersal and disappearance is common among ground squirrels (see Holekamp 1984a). With regard to intercolony dispersal, Boag and Murie (1981a) and Festa-Bianchet and King (1984) also noted a male bias in yearling dispersal of *S. columbianus* (6 of 7 intercolony dispersers of known sex were males). Similarly, Garrett and Franklin (in press) determined that intercolony dispersal of yearling black-tailed prairie dogs (*Cynomys ludovicianus*) was strongly male biased although female dispersal was not uncommon. Thus it seems that males are much more likely than females to disperse from their natal colony.

In summary, known and presumed intercolony dispersal was highly male biased and such movements were almost exclusively undertaken by the sexually immature yearling age class. Such a male bias in dispersal and disappearance of prereproductive individuals follows the pattern most commonly observed in other ground squirrel species (Holekamp 1984a) and for polygynous mammals in general (Greenwood 1980, Dobson 1982).

When did dispersal occur?

Disappearance and dispersal of yearlings occurred in all colonies studied. These losses were highly synchronous and occurred at roughly the same time each year (Fig. 2.2). The earliest known dispersal dates recorded were for two yearling males both natal residents of NFW. One male was last sighted at NFW on 4 June, 1984 and was subsequently recaptured at NFE on 9 June, 1984 (distance = 0.75km). The other male was last sighted 8 June, 1985 at NFW and was recaptured the next day at NFE. The latest known intercolony movement was made by an immigrant female first captured at NFE on 15 July, 1985 and later captured at NFW on 20 July, 1985. All other known dispersal and presumed dispersal movements of yearlings fell within the limits of these calender dates (4 June and 15 July - Fig. 2.3). Few yearlings disappeared from the study sites before or after this "dispersal period"; on average, fewer than 6% of yearlings disappeared outside the dispersal period (Table 2.2).

Since the precise timing of dispersal and disappearance (based on calendar date) was variable both within colonies between years and between colonies within years (Table 2.4), the maximum dispersal period based on known departure dates from different colonies in different years (Fig. 2.3) overestimates the duration of dispersal within a given colony in a given year. The average duration of the dispersal/disappearance period was only 15.8 days (range = 6-29) for yearling males and 10.3 days (range = 1-25) for yearling females (Table 2.4), but this apparent sex difference was not significant (paired t-test; $t = 1.476$; $n = 14$; $0.20 > P > 0.10$). Each year female yearlings disappeared from their natal colonies an average of 6 days later than their male counterparts (range 2-10 days) but again this difference only approached significance $t = 1.7746$; $n = 14$; $0.10 > P > 0.05$).

Median dispersal and disappearance dates for yearlings were positively correlated with median juvenile emergence dates; the later juveniles emerged in a given year, the later yearlings disappeared in that year (Pearson correlation; $r = 0.752$, $n = 14$, $P < 0.05$). There was also a positive but not statistically significant relationship between the duration of the disappearance period and the duration of the period over which juveniles emerged ($r = 0.352$,

Fig. 2.2. Timing of yearling disappearance from Columbian ground squirrel colonies NFW and NFE during 1985 and 1986.

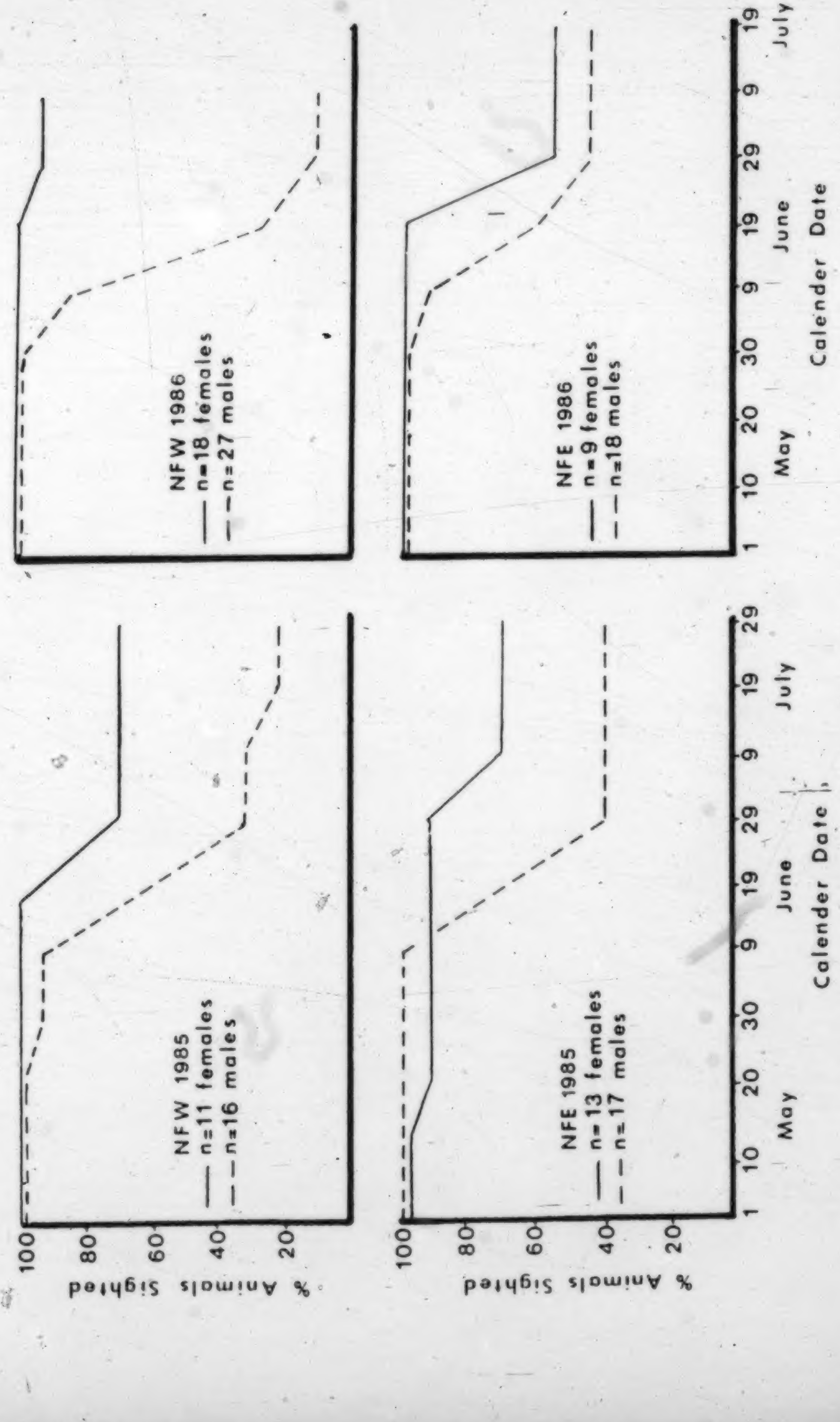

NFW 1985
— n=11 females
-- n=16 males
NFE 1985
— n=13 females
-- n=17 males
NFW 1986
— n=18 females
-- n=27 males
NFE 1986
— n=9 females
-- n=18 males
% Animals Sighted
100
80
60
40
20
1
10
20
30
9
19
29
9
19
29
May
June
July
Calender Date

Fig. 2.3. Disappearance dates (dates last sighted) for intercolony dispersers from Category 1 colonies of Columbian ground squirrels.

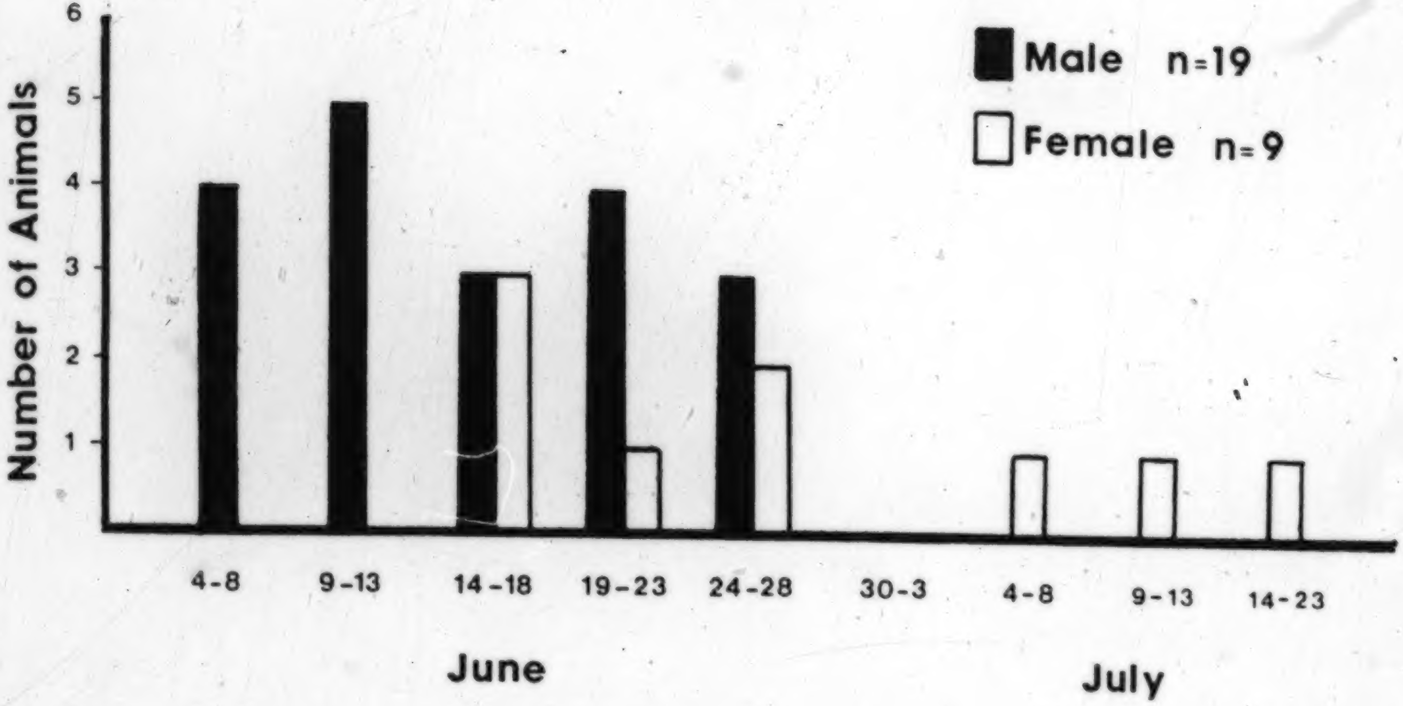

Number of Animals
6
5
4
3
2
1
Male n=19
Female n=9
4-8
9-13
14-18
19-23
24-28
30-3
4-8
9-13
14-23
June
July

Table 2.4 Timing of disappearance of yearling Columbian ground squirrels during the dispersal period in category 1 colonies.

Colony/ year	Sex (N)	Median disappearance date	Range	Duration in days
DC 1979	Male (4)	16 June	11-28 June	17
	Female (2)	-	23 June-4 July	11
DC 1980	Male (18)	18 June	8-30 June	22
	Female (6)	28 June	16 June-2 July	16
DC 1981	Male (9)	24 June	8 June-6 July	28
	Female (5)	29 June	25 June-7 July	12
DC 1982	Male (5)	30 June	25 June-8 July	13
	Female (1)	-	26 June	-
DC 1985	Male (4)	26 June	17-30 June	13
	Female (3)	28 June	27 June-7 July	10
RG 1984	Male (7)	19 June	13 June-5 July	7
	Female (-)	-	-	-
RG 1985	Male (8)	23 June	17-27 June	8
	Female (3)	26 June	25-28 June	3
RG 1986	Male (9)	15 June	14-28 June	9
	Female (-)	-	-	-
NFW 1984	Male (19)	16 June	4 June-5 July	29
	Female (9)	25 June	14 June-9 July	25
NFW 1985	Male (10)	19 June	8-27 June	19
	Female (5)	21 June	15-25 June	10
NFW 1986	Male (23)	16 June	5-25 June	20
	Female (1)	-	24 June	-
NFE 1984	Male (3)	25 June	23-29 June	6
	Female (2)	-	19-27 June	8
NFE 1985	Male (19)	23 June	12-28 June	16
	Female (3)	1 July	1 July	1
NFE 1986	Male (10)	15 June	7-21 June	14
	Female (4)	24 June	21-27 June	7
Total	Male (148)	19 June	4 June-8 July	$\bar{x}=15.8$
	Female (44)	26 June	14 June-9 July	$\bar{x}=10.3$

$n = 14$, $P>0.05$). Individual dispersal dates for yearlings were positively correlated with the dates of emergence of their mother's litter ($r = 0.27$, $n = 84$, $0.05>P>0.01$) and the emergence of their nearest neighbour's litter ($r = 0.38$, $n = 128$, $0.05>P>0.01$). However, only 7% of the variation in individual yearling disappearance date could be explained by the variation observed in emergence date for their mother's new litter. Twice as much (14%) of the variation in individual disappearance dates could be explained by the variation in emergence date of the yearlings' nearest neighbour's litter. This result is not surprising since most yearlings did not live near their mother at the time of juvenile emergence but instead occupied "communal areas" that were often surrounded by unrelated adult female neighbours (Chapter 3). Adult female aggression, possibly a means of protecting newly emerged juveniles (Festa-Bianchet and Boag 1982), peaked at this time and, along with aggression from adult males and yearling conspecifics, may have stimulated dispersal (Festa-Bianchet and King 1984, Hackett 1987, Chapter 4). The correlation that existed between date of a mother's litter emergence and date of departure of her yearling offspring probably resulted from the general synchrony of juvenile emergence.

Festa-Bianchet (1982) and Festa-Bianchet and King (1984 - whose timing data are included in this analysis) also found dispersal and disappearance from colony DC to be synchronous, of short duration, and to correspond with juvenile emergence. On the other hand, Boag and Murie (1981a) and Hackett (1987) found dispersal (equivalent to intra- *plus* intercolony dispersal-see Chapter 3) to be less synchronous and of longer duration than reported here. For instance, Boag and Murie recorded dispersal of yearlings as early as 22 May to 3 June and as late as 14 to 16 July with the majority of movements occurring in June and early July roughly coinciding with juvenile emergence. Similarly, Hackett (1987) noted that the majority of his animals dispersed in a 4-week period between mid-June and mid-July. I recorded intracolony dispersal movements of yearlings over most of the active season from just after emergence in the spring until 30 days before immergence in late summer (Chapter 3). Although these known intracolony dispersal movements occurred over the entire season, most moves coincided with juvenile emergence (Chapter 3). Thus, for *S. columbianus*, long-distance intercolony dispersal occurred within a relatively short time frame (usually less than 3 weeks) and coincided with juvenile emergence, whereas shorter distance intracolony movements occurred at almost any time during the yearlings' active season but mostly near the time when juveniles first emerged above ground.

Garrett and Franklin (in press) also noted differences in timing between inter- and intracolony dispersal of yearling black-tailed prairie dogs, *Cynomys ludovicianus*. Intercolony dispersal was synchronous and occurred mostly over a 2-week period coinciding with juvenile emergence. On the other hand, intracolony movements were not synchronous and occurred over the entire annual cycle. Garrett and Franklin postulated that yearling *C. ludovicianus* may time emigration from the natal colony to coincide with the time when vegetative standing crop is greatest to give food and cover in transit. I argue elsewhere (Chapter 5) that the timing of intercolony dispersal by *S. columbianus* is tied more to weight and body condition than to physiognomic features of the environment. Although dispersal (intra- and intercolony) of yearling Columbian ground squirrels does not seem to be triggered by the attainment of some critical body weight (Hackett 1987) as may be the case for Belding's ground squirrels (Holekamp 1983, 1986; but see Hackett 1987), a critical minimum body mass does seem necessary before *S. columbianus* will undertake an intercolony movement (Chapter 5). Such a critical minimum body weight was achieved by the time of juvenile emergence for most yearlings in C1 and C2 colonies. On average, heavier animals dispersed before lighter ones and the smallest animals often delayed dispersal until they were 2-years old (Chapter 5). Moreover, female yearlings, which are lighter than male yearlings and gain less weight per day (Boag and Murie 1981b), dispersed from colonies on average 6 days later than male yearlings. Yearlings that reached the critical body mass after juvenile emergence probably did not disperse from the colony because the proximate stimulus of dispersal (conspecific aggression) had been removed (Hackett 1987 and Chapter 4). On the other hand, intracolony dispersal movements are not correlated with weight of yearlings (Hackett 1987 and Chapter 5), possibly because such short distance moves are not energetically taxing.

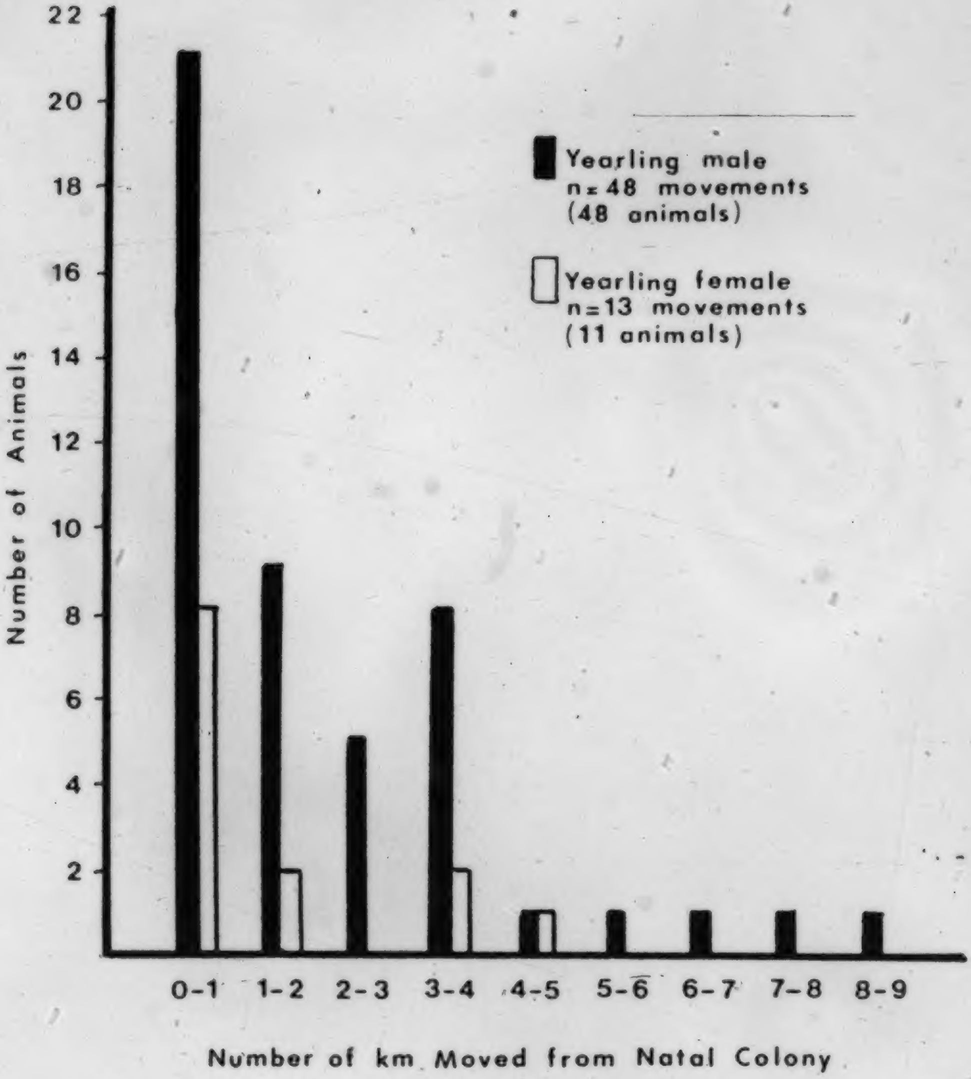
How far did animals disperse?

Nearly one-half (48%) of the 61 intercolony dispersal movements recorded for yearlings occurred between colony pairs that were separated by less than 1 km (NFW/NFE and AA/AB - see Fig. 2.1 and 2.4). Dispersal movements between colonies 1 to 4 km apart accounted for an additional 43% of all yearling intercolony exchanges, and the remaining 10% of dispersing yearlings moved to colonies greater than 4 km distant (Fig. 2.4). Intercolony dispersal distances of males (2.0 km) and females (1.8 km) did not differ significantly (Mann-Whitney U Test; $P>0.20$). The greatest straight-line dispersal distance recorded was 8.5 km for a yearling male that dispersed from his natal colony (WP) to NFE (Fig. 2.1). The greatest distance recorded for a female yearling was 5.0 km for an animal that dispersed from NFW to the northwest edge of HM in 1983 (Fig. 2.1).

These distances were straight-line minimum estimates; the actual distance travelled by a squirrel was probably considerably greater. Garrett and Franklin (in press) found that straight-line measures of dispersal accounted for only 80% of the actual distances moved by yearling black-tailed prairie dogs. The disparity between actual and straight-line measures of dispersal in this study were probably greater than 80% because of the mountainous terrain and the meandering of probable routes of movement between colonies along trails and drainages (see below).

Distances moved by intercolony dispersers are necessarily dependent on the patch structure of suitable habitat in the surrounding area. In areas where suitable ground squirrel habitat is widely scattered and relatively common, intercolony dispersal distances may be small if colonies exist nearby such as in the case of colony pairs AA-AB and NFE-NFW. Thus comparisions of differences in distance moved before settling for different ground squirrel populations (and ground squirrel species) may often be a function of habitat structure or site availability rather than of differences in biology.

Fig. 2.4 Distance moved by yearling Columbian ground squirrels: male and female intercolony dispersers.


22
20
18
16
14
12
10
8
6
4
2
Number of Animals
Yearling male
n=48 movements
(48 animals)
Yearling female
n=13 movements
(11 animals)
0-1
1-2
2-3
3-4
4-5
5-6
6-7
7-8
8-9
Number of km Moved from Natal Colony

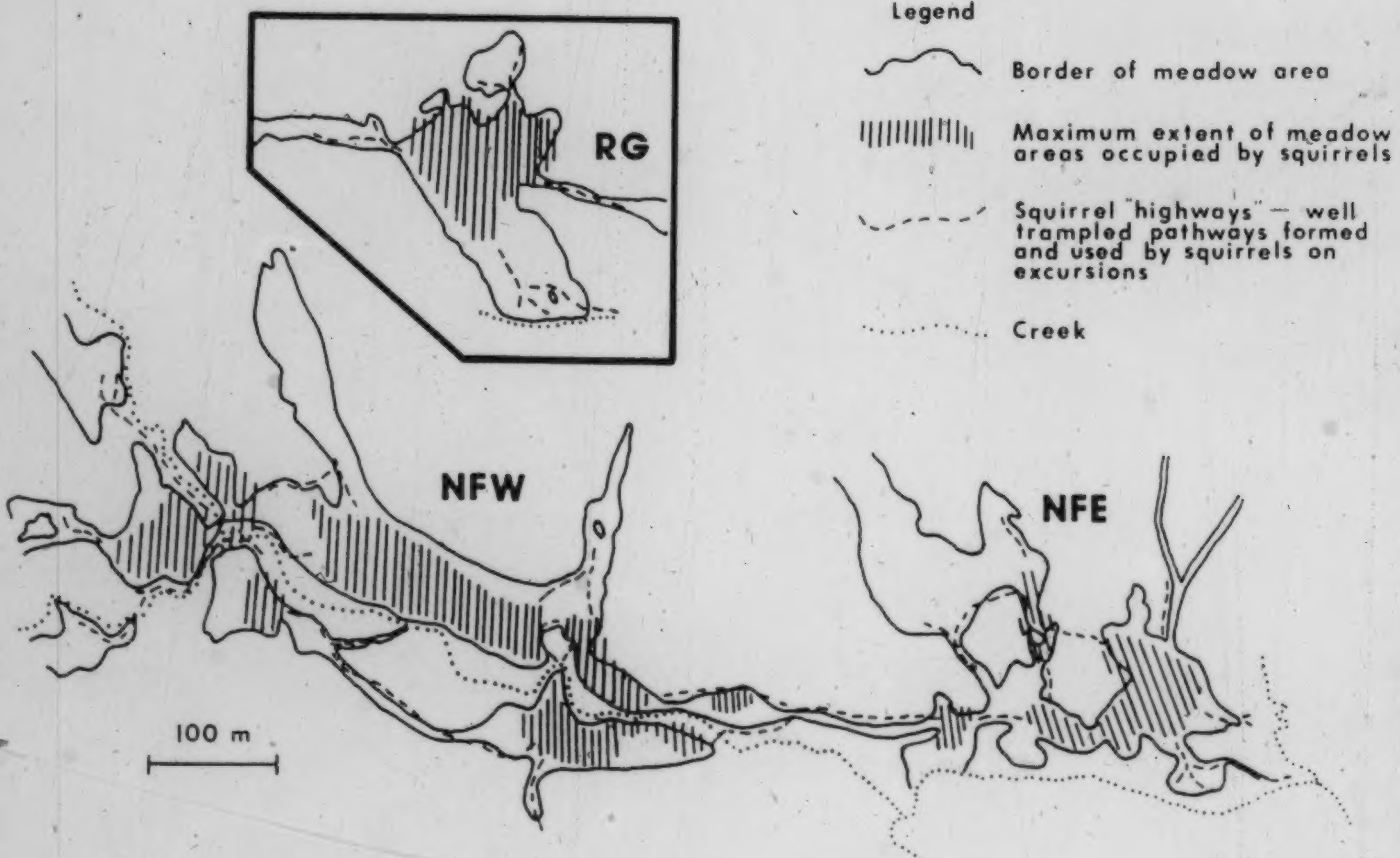
A sex difference in distance dispersed between colonies was not observed possibly because habitat structure determined how far animals would have to move to locate other areas of suitable habitat. The distribution and availability of suitable habitat patches nearby should be the same for all animals leaving a given colony (or moving within a colony for that matter) regardless of the sex and/or age of the departing animal.

How were intercolony movements accomplished?

Of the 325 yearlings recorded disappearing during the dispersal period from C1 and C2 colonies (n = 51 colony years) only 21 of these animals should have encountered another colony (given perfect survivorship in transit) under the assumptions of the RLM model (see Methods for details of assumptions and calculations). The observed number of intercolony exchanges between colony pairs less than or equal to 4 km apart was 43 animals; significantly more than expected $X^2 = 22.82$, $P<0.001$). This result suggests that dispersing animals are more likely to encounter another squirrel colony than would be predicted on the basis of random, linear movements. Thus at least some squirrels must disperse in a manner that enhances their chances of encountering other colonies.

Sightings and recaptures of animals making excursions at NFW, NFE, and RG indicated that direction of movements away from colonies were not random but rather tended to follow pathways, drainage systems, and topographic features (Fig. 2.5). At the time of dispersal, squirrels were often sighted making excursions to colony edges and into the forested regions surrounding a colony. Once away from the safety of colonial burrow systems, squirrels were observed seeking shelter under logs, roots, overhanging vegetation and dense shrubbery. In addition, squirrels on excursions often used pocket gopher (*Thomomys talpoides*) burrows or red squirrel (*Tamiasciuris hudsonicus*) middens. Movements of such ground squirrels were characterized by quick darts between areas of cover followed by long visual scanning at temporary refuges. Often animals moved away from the colony for some distance only to return before nightfall. The next day the same animal would return to the

Fig 2.5. Extent of meadow areas occupied and location of pathways used by Columbian ground squirrels at NFW, NFE, and RG (*cf* Fig. 2.1).


Legend
Border of meadow area
Maximum extent of meadow areas occupied by squirrels
Squirrel "highways" — well trampled pathways formed and used by squirrels on excursions
Creek
RG
NFW
NFE
100 m

same pathway, often travelling further away than the day before. After several days of increasingly distant excursions, the squirrel would disappear, never to be seen again, or in some cases to be recaptured or resighted at a different colony.

Often more than one individual used the same pathway and refuge and in so doing created a well trampled squirrel "highway"(*cf* Shaw 1924). Several such routes existed at NFE, NFW, and RG (Fig. 2.5) as well as at AA and AB. The highways at NFE, NFW, AA, and AB often followed stream banks and trails. For instance, AA and AB are bordered on the southeast by steep cliffs of the Sheep River. Along most of the meadow-cliff interface, overhanging vegetation forms a tunnel-like runway which the squirrels used when moving between these two colonies.

Many researchers have documented long distance dispersal of ground squirrels: 1.4 km for *Spermophilus parryii* (McLean 1982), 4.0 km for *Marmota flaviventris* (Svendson 1973), 6.7 km for *Cynomys ludovicianus* (Garrett and Franklin in press), 6.7 km for *S. columbianus* (Boag and Murie 1981a) and 9.6 km for *S. richardsonii* (Quantrom 1971). Few, however, have speculated on how such movements were accomplished. Trail following has been reported for dispersing black-tailed prairie dogs (Koford 1958, Garrett *et al.* 1982, Knowles 1985) and has been postulated for Columbian ground squirrels (Hackett 1987). Garrett and Franklin (in press) followed radiocollared *C. ludovicianus* and found that the animals used vegetated ravines and canyons (drainage topography) to move between colonies. Knowles (1985) reported that of 38 "extra-town" dispersers observed all but one were sighted travelling on a road or vehicle trail of some sort. In my study, the use of drainage topography, trails, or roads by dispersing squirrels would be a highly successful tactic for locating new ground squirrel colonies as much ground squirrel habitat is adjacent to waterways and trails - Fig. 2.1). Further radio telemetric studies are necessary to document precisely how such intercolony movements are made and to determine the types of transit strategies used.

How successful were intercolony dispersers?

Of 250 male and 75 female yearlings that disappeared from C1 and C2 colonies, 40 (16%) males and 8 (11%) females were known to have moved successfully between colonies. These numbers represent minimum known survival rates as some marked animals probably dispersed successfully to unstudied populations. An estimate of total survival rate in transit could be calculated as the number of known intercolony dispersers plus the estimated number of successful dispersers that emigrated to unstudied populations. The number of marked animals that dispersed to unstudied populations could be estimated on the basis of the proportion of marked to unmarked animals that immigrated into the study populations. Such an estimate assumes a roughly equivalent exchange of animals between marked and unmarked populations - likely an invalid assumption. For instance, 5 of the 13 (39%) presumed intercolony dispersers from NFE dispersed to NFW in 1985 whereas only 1 of 15 (7%) yearlings that disappeared from NFW in 1985 was later recaptured at NFE. In 1986, 6 of 24 (25%) yearlings dispersed from NFW to NFE whereas 3 of 14 (21%) yearlings made the reverse movement.

A better estimate of total survival in transit can be determined based on the ratio of 2-year-old natal residents versus 2-year-old immigrant residents. In colonies where the resident status of all or nearly all 2-year-old animals was known, 58% of adult males were natal residents and 42% were immigrant residents (*n* = 210). For adult females 91% were natal residents, 9% were immigrant residents (*n* = 224). For every 100 males born in a colony that survive to be yearlings, 22 will be expected to be present as 2-year-olds the following spring (0.26 = rate of male philopatry multiplied by 0.83 = yearling male resident overwinter survival rate *n* = 66). These 22 animals will represent on average 58% of the 2-year-old population, the other 42% (or 16 animals) will be composed of immigrant residents. Of the 100 male yearlings originally present, 74 will disperse (disappear) from their natal colony and only 16 of these (on average) will be alive as 2-year-olds in other colonies. Since the average survival rate of these immigrant yearling males to age 2 is known (0.88, *n* = 58) then it is simply a matter of solving for the unknown; in this case survival during the dispersal move ($16/0.88 = x/100 = 18.2$; $18.2/74 = 0.246$). A 25% rate of survival during dispersal between colonies for yearling males is necessary to explain the observed ratio of adult male natal residents to immigrant residents. For females a 30% survival rate is necessary to explain the ratio of natal to immigrant residents observed in C1 and C2 colonies.

Few data appear in the literature documenting success rate in transit for dispersing mammals; in most cases authors have supposed that dispersal movements must be risky and that few animals were likely to be successful (see references in Hackett 1987). Garrett and Franklin (in press) reported that intracolony dispersal of black-tailed prairie dogs was a low risk venture (relative to survival) because no in-transit mortality was observed. Similarly, Hackett (1987) noted no mortality in transit of dispersing yearling Columbian ground squirrels over areas of continuous habitat. Hackett suspected that dispersing yearlings were successful because they were extremely wary while in transit, moving rapidly from burrow to burrow and taking refuge at the first sign of danger.

On the other hand, Garrett and Franklin found intercolony dispersal to be much more risky with 15 (54%) of 28 disperser's dying during the dispersal period (whether or not these deaths occurred in transit is not clear from their presentation). My estimates of 25% survival in transit of male and 30% survival of female intercolony dispersers suggest that, although dispersal across areas of inhospitable habitat (in this case forested mountain terrain) is risky, it is not as dangerous as was previously supposed (Lidicker 1975, 1978, Tamarin 1978, Schmutz *et al.* 1979, Gaines and McClenaghen 1980). Radio-telemetry studies of dispersing animals from small isolated ground squirrel colonies will be necessary to determine actual mortality rates in transit for intercolony dispersers and the relative importance of variables such as the distance and dispersion of neighbouring habitat patches, and the nature and size of the intervening habitat that must be traversed by a dispersing animal.

Summary

Intercolony dispersal was confined mostly to yearlings. The few adults that dispersed to other colonies were either delayed natal dispersers, artificially transplanted animals, or animals that lived nearby and were familiar with an adjacent colony. Among yearlings, males were the most frequent dispersers to other colonies. Intercolony dispersal was synchronous within colonies and coincided with juvenile emergence. Yearling females that dispersed from the natal colony tended to leave slightly later than yearling males. Most animals recorded as having dispersed in this study moved to colonies less than 4.0 km away but movements of up to 8.5 km were recorded. There was no difference between male and female yearlings in final distance dispersed. Dispersing yearlings apparently left the natal colony in non-random directions, probably following features such as trails and drainage systems. Such movement would probably enhance their chances of successfully locating nearby squirrel colonies. Minimum known survival rates while in transit were 16% for yearling males and 11% for yearling females. Estimates of actual survival rate in transit were 25% for males and 30% for females.

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III. Adult-Yearling Spatial Relations and Spatial History of Individuals in Relation to Habitat Structure and Natal Dispersal in the Columbian Ground Squirrel

Introduction

Individual animals living in different populations may face different environmental constraints (Bronson 1979, Johns and Armitage 1979, Webb 1981, Murie 1985, Zammuto and Millar 1985, Dobson and Murie 1987). Different environmental constraints may "force" the members of different populations to adopt varied life history strategies (Dobson and Murie 1987) which in turn may result in the expression of varied social and spatial relationships. For example, Webb (1981:175) reported that dispersal of yearling yellow-bellied marmots (*Marmota flaviventris*), inhabitating areas of continuous habitat, occurred without evidence of agonism, whereas dispersal of yearlings from patches of discontinuous habitat occurred only after brief periods of intense agonistic interactions with sibling(s) and parent(s). Webb concluded that "when the animal is reluctant to disperse because of a combination of high transit difficulty and low desirability of a new site, antagonistic social interactions with relatives force dispersal". Had Webb only studied marmots in "continuous" habitat, he would have concluded in all probability that agonism was not necessary to force dispersal. Obviously generalizations about social behaviour and social organization should be made only after a number of populations (*sensu* Slade and Balph 1974) have been studied.

Hackett (1987) studied the spatial and social relations of yearling and adult Columbian ground squirrels (*Spermophilus columbianus*) in continuous habitat in southwestern Alberta. Hackett concluded that the proximal cause of dispersal among yearlings was conspecific aggression from family members on the natal home range. Reproductively active mothers apparently forced yearlings off the natal home range while siblings competed to remain on or near the natal area (sisters usually outcompeted brothers). Festa-Bianchet and King (1984) reported that yearling Columbian ground squirrels of both sexes often formed "groups" away from the natal home range where yearlings came to play.

Festa-Bianchet and King called these areas "playgrounds". Playground groups were often composed of six to seven individuals of mixed sex and included both siblings and nonsiblings. As well, adult males in the Festa-Bianchet and King study apparently were more spatially associated with yearlings than they were in Hackett 's study. Two questions are raised: 1) why were there differences in the spatial relations among adults and yearlings in the two studies? and 2) does conspecific aggression from family members (or non-family members for that matter) force dispersal of yearlings under all variations of social and spatial relations (that is, is the proximal cause of dispersal the same in all populations)?

This chapter documents the spatial relations and social organization among adult and yearling Columbian ground squirrels that inhabited three, relatively small, isolated populations in southwestern Alberta. The observations presented here are compared with the findings of others who have studied spatial and social organization of Columbian ground squirrels in more "continuous" habitat (eg. Hackett 1987). The spatial (this chapter) and social (Chapter 4) relations among yearlings and between yearlings and adults are used to test the applicability of Hackett's conspecific aggression hypothesis to the populations I studied. As well, I document the spatial history of individual squirrels from birth to reproductive maturity. Detailed documentation of changes in use of space over time reveals the timing and extent of dispersal as well as the distribution of distances moved by dispersing individuals. Analysis of the spatial relations and spatial history of individuals relative to their natal site, to closely related kin, and to neighbouring conspecifics may help elucidate the nature of dispersal as a biological process, and what function(s) can be attributed to it. Finally, changes in use of space over time are considered in the light of various definitions of dispersal.

Methods

Discontinuous and continuous habitat have been defined and discussed previously (Chapter 2 and Appendix 1). Briefly, **continuous habitat** is any habitat containing essential resources (eg. food, burrow systems, hibernacula) that is physically large enough to enable any individual in the population to undergo an intracolony dispersal movement in at least two directions, whereas **discontinuous habitat** is physically too small to allow intracolony dispersal in two directions. **Intracolony dispersal** is defined in the discussion section of this chapter. The criteria used to differentiate between a "disperser" and a "nondisperser" are best considered in terms of the actual distribution of movements recorded rather than on some set of arbitrary *a priori* criteria and as such the definition of dispersal is discussed in this chapter after the results of individual spatial histories are given.

The use of space by individual Columbian ground squirrels was studied at three sites (NFW, NFE, and RG - Figs. 2.1, 2.5 and Table 2.1, Chapter 2) over 3 years (1984-1986) in the Sheep River-Gorge Creek drainage of southwestern Alberta. All animals at each site (colony - for definition see Chapter 2) were individually identifiable by numbered eartags and unique dyemarks applied when the animals were live-trapped (Chapter 2). Sex and age (or minimum age) were known for all animals present and reproductive status and body weight were recorded regularly (Chapters 2 and 5). Maternal relationships were known for all animals born in each colony during the course of the study (Chapter 2).

Location of captures and sightings of animals within a colony were estimated to the nearest meter on the x and y coordinates of a grid system established at each colony at the initiation of the study. Coloured plastic flags on wires were used to mark the corners of each 10 x 10 m grid square.

Observations were conducted from 2-3 m high observation towers (one in each colony) and squirrels were observed with 10 x 50 binoculars and 20-45 x 60 spotting scopes. Each morning, observations were initiated when the first squirrel emerged (usually between 6:00-7:00 am MST) and were continued until 3 hours had lapsed. A 3-hour morning observation period was chosen because it represented the time when the greatest number of squirrels were simultaneously active above ground (person. obs.). At NFW 21% of the squirrels lived in peripheral locations away from the main colony area and at NFE 33% did so. These animals could not be observed readily from the observation stand (see Appendix 2).

Animals in peripheral areas were observed during short 15-30 minute "peripheral" scans that usually followed the 3-hour observation of the main colony area. During the dispersal period (Chapter 2), peripheral scans were also conducted in the evenings approximately 2 hours before evening immergence of squirrels. These sightings facilitated documentation of pathways used by squirrels on excursions (Chapter 2) and were useful for documenting home range shifts of centrally-located animals to points at the periphery and vice-versa. In total, squirrels were observed for 1748.75 h on 599 days (1420.25 h on the "main" areas and 328.5 h on "peripheral" areas - Appendix 3). Observations were not conducted when weather conditions greatly reduced the above ground activity of squirrels (eg. during rain, snow, or extreme heat).

The identity, location, and activity of each squirrel sighted as well as any social interactions in which an animal was involved were recorded. A "focal-scan" sampling regime was used to provide accurate information on rates of social interaction (see Chapter 4 and Appendix 4 for details and discussion).

Date of breeding for females could be estimated to within 1-2 days based on the physical appearance of the vulva, the presence of copulatory plugs, and the behavioural response of adult males to the female in question (Murie and Harris 1982). Females, the breeding date of which had been estimated in this manner, were captured and handled repeatedly over a 7-day period centered on the estimated date of parturition - 24 days (the gestation period of Columbian ground squirrels - Murie and Harris 1982) after the estimated date of conception. Evidence of parturition (marked weight loss and open, moist, or bloody vulva) for females was gathered during this period of intensive trapping. Date of parturition for 15 females was known to within 1-2 days using this method. For these 15 females, juveniles emerged above ground 25-30 days later (x = 27.6 days). Since this observation was similar to that of others (see Ferron 1984 for review), I used 28 days as the duration of the underground lactation period. For those females with unknown dates of breeding and parturition, these dates were estimated by backdating 52 and 28 days respectively from the date of juvenile emergence.

For purposes of analysis, the active season at each colony was divided into 10-day intervals. Intervals of ten days were chosen because 10 days was the minimum amount of time required to obtain an average of 30 sightings per animal which I considered to be an adequate sample size for determining the size of a home range (Appendix 5), a 10-day time frame was small enough to detect subtle shifts in home range location and to determine accurately the timing of such shifts, and division into 10-day intervals was consistent with the intervals used in analyses by other researchers (eg. Waterman 1986, Hackett 1987).

In dividing the active season of each colony into 11 10-day intervals, I used the median date of juvenile emergence for each colony as a time marker and arbitrarily called it Day 60 of the 110 day season. In this way all colonies were aligned to a common biological event in the active cycle which facilitated intercolony (and interyear) comparisons. Hackett (1987) also aligned his sites to a common day on the basis of juvenile emergence. He set the first day of litter emergence at each site to correspond to day 50. Of 158 litters emerging at NFW, NFE, and RG from 1984-1986, 136 (86%) emerged between days 53 and 65, similar to those of Hackett (1987 - Days 50 to 63). Thus the day numbers used by Hackett essentially correspond to the day numbers I used in this study.

The events in the annual cycle relative to the 10-day intervals, were as follows: Period E (days 0-9) included the time of emergence from hibernation (Appendix 6). As well, it coincided with the period of breeding; 86% of all females present bred between days 1 and 13 (median = day 8). Most females gave birth between days 25 and 37 (late Period 2 and early Period 3). Juvenile emergence occurred mostly during Periods 5 and 6 (days 53 to 65, see above). Adult squirrels began to immerge into hibernation in Period 10 (days 100 to 109).

In 1984 observations began during Period 1 at NFE, Period 2 at NFW, and Period 3 at RG and continued until immergence began in Period 10. During 1985 and 1986 observations were initiated as soon as squirrels were emerging from hibernation (Period E in all cases) and were continuted until immergence began in 1985 (Period 10) or until the end of dispersal

(Period 7 - Chapter 2 and below) in 1986.

Sizes of home ranges were calculated as minimum convex polygons (Mohr 1947) using a special version of the MIDAS CARTOGRAPH programme written by Dan Fox at the University of Michigan, Ann Arbor. Home range was defined as that area covered in normal daily activities (Lehner 1979). Waterman (1986) suggested that in calculating home range, the outermost 20% of points be discarded since the area encompassed by the innermost 80% of points best indicated where the animals spent most of their time. Waterman's conclusion is consistent with that of Davis (1982) and Hackett (person. comm.). Thus I eliminated the outermost 20% of sightings; the remaining 80% encompassed what I considered the animal's home range for that period. The minimum number of sightings used to calculate home range was 30 (24 after the outermost 20% of sightings were dropped). Percent of home range overlap between adjacent squirrels was calculated as the total area of mutual overlap divided by the total home range size of each of the squirrels involved.

The spatial history of Columbian ground squirrels captured as juveniles in 1984 and 1985 was followed to Period 7 of 1986. As well the spatial history of the 1983 juvenile cohort was followed beginning in 1984 when the squirrels were yearlings until Period 7 of 1986. Thus the spatial history of individual animals born in 1983, 1984 and 1985 was known until the animals were 3, 2 and 1-year old, respectively.

Changes in use of space over time for individual animals were analysed by comparing distances between activity centres (see below) from one 10-day period to the next, documenting distance moved from the birth site or "natal burrow" (Harris and Murie 1984), and by comparing distances between an individual's activity centre and the activity centre of its mother over time. Centres of activity (centroids) were calculated as the mean x and y coordinate of all sightings within the 80% home range and as such do not necessarily represent a biologically "important" point in space. Rather, activity centres, like any mean, are merely "representative" values. Activity centres represented in a single point in space the centre of the general area in which an animal lived.

The proportion of animals shifting activity centres during each 10-day period was followed for individuals representing the juvenile cohorts of 1983, 1984 and 1985. Squirrels were considered to have shifted their home ranges when the distance between activity centres of adjacent periods equaled or exceeded the average of maximum home range diameters for animals of the same age and sex class (Appendix 7). Thus, females of all age and sex categories were considered to have shifted their home ranges when the distance between adjacent activity centres equalled or exceeded 25 m. The distance criteria for juvenile and yearling males was 30 m and for adult males 40 m (Appendix 7). Natal home range was arbitrarily defined as a circle in which the centre was the opening to the natal burrow and the diameter was equal to one juvenile home range diameter.

During the course of this study, 29 of the 107 yearling females present in the colonies bred. Yearling females that breed behave differently than nonbreeding yearlings (Festa-Bianchet 1981; Chapter 4) and therefore patterns of space use and the spatial history of these two groups were analysed separately.

A vegetation analysis was conducted at each colony in early June 1985 to compare vegetative cover on "communal" areas used by yearlings (see below) with cover on adult female "territories". At each colony, two communal areas and five female territories (each chosen at random) were used for the analysis (except at RG where only one communal area existed). For sampling purposes, a female "territory" was arbitrarily defined as a circle with the origin at the natal burrow and a diameter of 25 m. The vegetation within each "territory" was randomly sampled 10 timesusing a 2 x 5 dm rectangle after Daubenmire and Daubenmire (1968). Percent cover was defined as the proportion of the rectangle covered bt the vertical projection of the edges of the plants to the ground surface. The total percent cover for a given territory was calculated as the average of the 10 samples. Two 10 x 10 m grids were randomly chosen from within each yearling "communal" area; each grid was randomly sampled five times with the 2 x 5 dm rectangle and the average of the 10 samples was considered the percent cover score for the communal area as a whole.

Nonparametric statistical inference was used because the data sets did not meet the assumptions of parametric inference; data were not independent, homoscedastic, or normally distributed (Sokal and Rohlf 1981). In addition, the results of the nonparametric tests presented herein should be viewed cautiously because of the increased probability of a Type I error occurring where independence of samples is not assured (eg. most ethological data - Machlis *et al.* 1985).

Results

Demographic characteristics

Population structure and density at the three colonies studied is given in Appendix 8 and 9. At all three colonies spring population size increased from one year to the next yet densities remained constant with the exception of NFW where densities decreased over time (Appendix 9). A constant or declining density in the face of an expanding population was only possible through expansion of the colonies in space (Appendix 9). Spring populations in 1986 were 1.9, 1.8, and 1.3 times larger than 1984 populations at RG, NFE, and NFW respectively. Densities at NFE and RG in 1986 were similar to densities recorded in 1984 but at NFW density in 1986 was 0.5 of that in 1984.

In ~~1986 a~~ number of adults was either removed from or added to each colony in an attempt to determine how the presence or absence of mothers, and the density of adult males affected likelihood of yearling dispersal (see Chapter 6 and Appendix 8). These removals reduced spring population size in 1986 by 17.0% at RG, 21.0% at NFE, and 2% at NFW (Appendix 8). In spite of the removals absolute population levels in all 3 colonies remained high relative to levels recorded in 1984 and 1985 (Appendix 8).

Of the 102 yearling females that emerged on the study areas, 29 (28%) bred and showed signs of lactation (swollen nipples); 21 of these 29 (72%) brought litters above ground (Appendix 8). Nearly all (27/29 ~93%) of these pregnancies occurred in 1986.

Most yearling males (101/139 ~73%) that emerged on the study areas disappeared (presumably dispersed see - Chapter 2) from their natal colony whereas most yearling females (74/102 ~73%) remained in their natal colony (Table 3.1). For both male and female yearlings disappearance from colonies was variable among years and between colonies (Table 3.1).

None of the 29 yearling females that bred disappeared from the colonies during the dispersal period. This is in contrast to the 38% loss recorded (28/73) for nonbreeding female yearlings (Table 3.1).

General description of adult-yearling spatial relations

Most squirrels (77%) emerged from hibernation before or during Period E (Appendix 6 - newly emerged animals could be distinguished by flakes of skin in the pelage - Murie and Harris 1982). Emergence differed among sex and age categories; adult males emerged first (76% were active above-ground before Period E) followed by adult females (25% emerged before Period E) and yearlings (6% of males and 5% of females emerged before Period E - Appendix 6). At all three colonies (NFW, NFE, and RG), most animals (89%) emerged from one of the several "common" hibernacula areas located in each colony (see Appendix 10 for further details).

Adult female home ranges extensively overlapped during Period E (breeding); an example from colony NFE is given in Fig. 3.1. During this time most home ranges were located on areas encompassing hibernacula. Adult males held large discrete home ranges that overlapped little those of other adult males but overlapped extensively those of several adult females (Fig. 3.1). As soon as females bred (Period E and early Period 1) they moved away from the hibernacula and established ranges elsewhere. By the time of parturition (late Period 2 and early Period 3) adult female's home ranges were much more widely scattered and almost exclusive (for a typical example see Fig. 3.2).

Table 3.1 Number of yearling Columbian ground squirrels dispersing (proportion in parentheses)[1] from three colonies (NFW, NFE, and RG) during 1984-1986.

	NFW			NFE			RG			Total	
	1984	1985	1986	1984	1985	1986	1984	1985	1986		
Females[2]	10/22 (0.45)	5/11 (0.45)	1/18 (0.06)	2/10 (0.20)	3/12 (0.25)	4/9 (0.44)	0/3 (0.00)	3/5 (0.60)	0/12 (0.00)	28/102 (0.27)	28/73[2] (0.38)
Males	19/24 (0.79)	10/15 (0.67)	23/27 (0.93)	5/8 (0.63)	10/17 (0.59)	10/18 (0.56)	7/7 (1.0)	8/8 (1.0)	9/15 (0.60)	101/139 (0.73)	

[1] Number of animals disappearing during the dispersal period/number of animals present at the beginning of the dispersal period (see Chapter 2 for details)

[2] Excludes yearling females that bred

Fig. 3.1. Home ranges (80% core areas) of adult male and female Columbian ground squirrels at colony NFE during Period E, 1986.

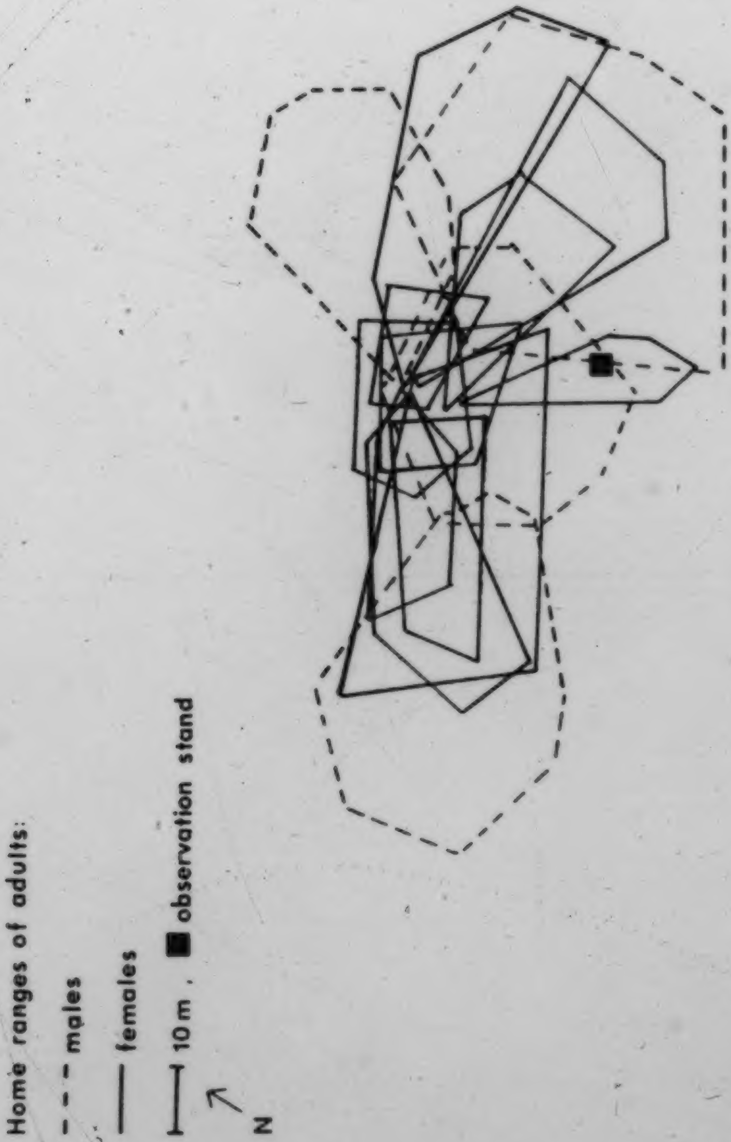
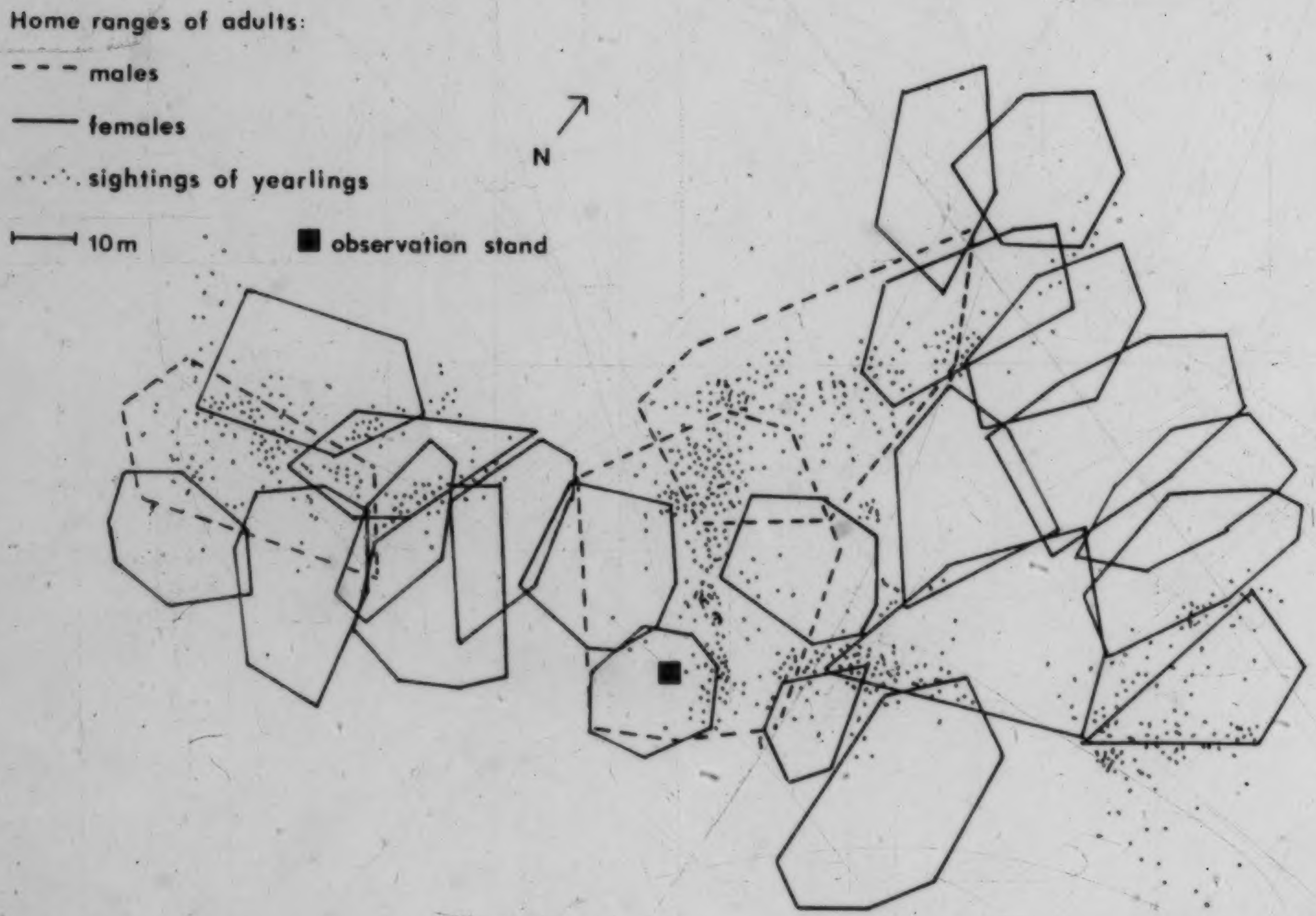

Home ranges of adults:
males
females
10 m
observation stand
N

Fig. 3.2. Home ranges (80% core areas) of adult male and female Columbian ground squirrels, and sightings of yearling males and females at colony NFF during Period 3, 1986.


Home ranges of adults:
males
females
sightings of yearlings
10 m
observation stand
N

Most yearlings emerged on the areas with hibernacula during Period E when adults were breeding and were beginning to move off these areas. By Period 3 most yearlings still resided on or near the hibernacula centre from which they emerged. By contrast, adult females generally did not have home ranges located on hibernacula centres during Period 3. A plot of the sightings of individual yearlings at NFE during period 3 in 1986 revealed that yearlings tended to live in the interstices among adult female home ranges (Fig. 3.2). This pattern was the same in all 3 colonies (NFW, NFE, and RG) and in all 3 years (1984-1986) of the study. At this time the home ranges of yearlings living on areas with hibernacula and in the interstices among adult female home ranges often overlapped extensively with those of other yearlings (Fig. 3.3 and 3.4). Usually large numbers of yearlings lived on relatively small areas and the density of animals on these areas was high relative that in the colony as a whole (*cf* Figs. 3.3, 3.4, and Appendix 9). Such areas containing high concentrations of overlapping yearling home ranges were termed yearling "communal" areas.

During Period 3 adult male home ranges were also located in the interstices between the more numerous female home ranges and often overlapped extensively the yearling communal areas (Fig. 3.2). In fact, adult male home ranges overlapped on average significantly more with yearling home ranges than with adult female home ranges reflecting adult male and yearling co-occurance on communal areas (Table 3.2).

The spatial relationships between adult males, females, and yearlings during Periods 2-5 were essentially the same as outlined above for Period 3; widely dispersed and separate adult female home ranges, concentrated yearling home ranges which overlapped one another extensively, and adult male home ranges located between adult female home ranges and overlapping to varying degrees the yearling communal areas.

During and after Period 6 (juvenile emergence) adult home range size and degree of overlap increased (Fig. 3.5 and below), yearling communal groups broke up, some yearlings emigrated from the colony (Chapter 2 and Table 3.1) while others shifted away from the communal area but remained in the colony (see below). During Periods 7-10 home ranges

Fig. 3.3. Outlines of the home ranges (80% core areas) of yearling Columbian ground squirrels present at colony NFE during Period 3, 1986.

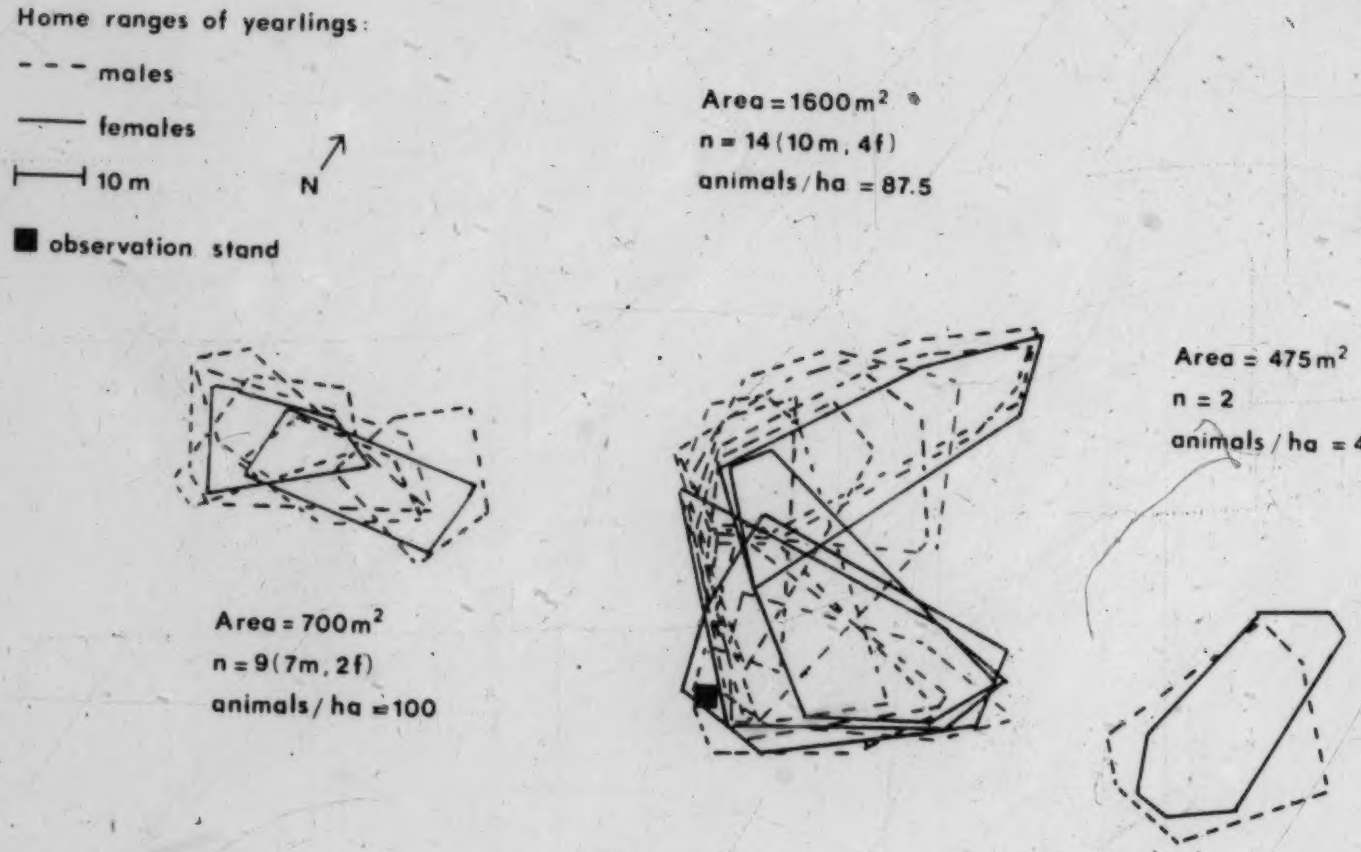
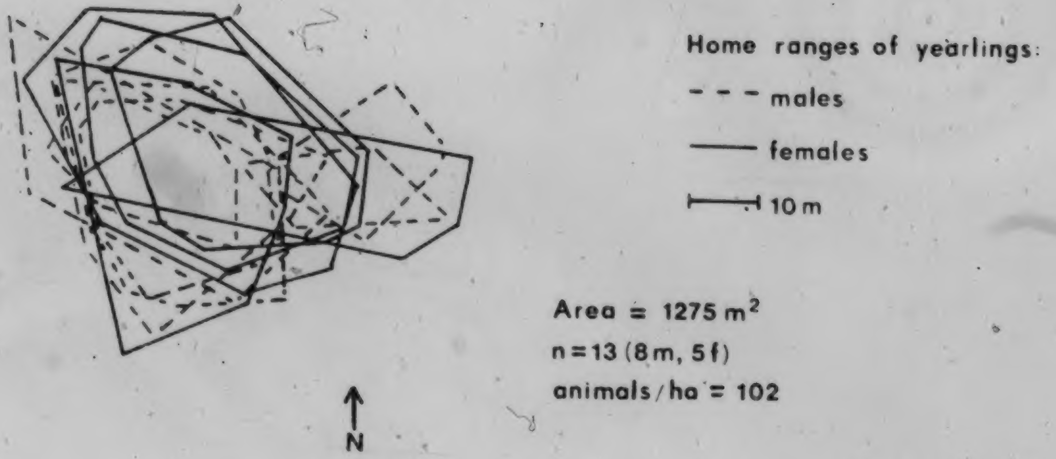

Home ranges of yearlings:
- - - males
——— females
10 m
N
■ observation stand
Area = 700m^2
n = 9(7m, 2f)
animals/ha = 100
Area = 1600m^2
n = 14 (10m, 4f)
animals/ha = 87.5
Area = 475m^2
n = 2
animals/ha = 42.1

Fig. 3.4. Outlines of the home ranges (80% core areas) of yearling Columbian ground squirrels present at colony RG during Period 3, 1985.


Home ranges of yearlings:
- - - males
—— females
10 m
N

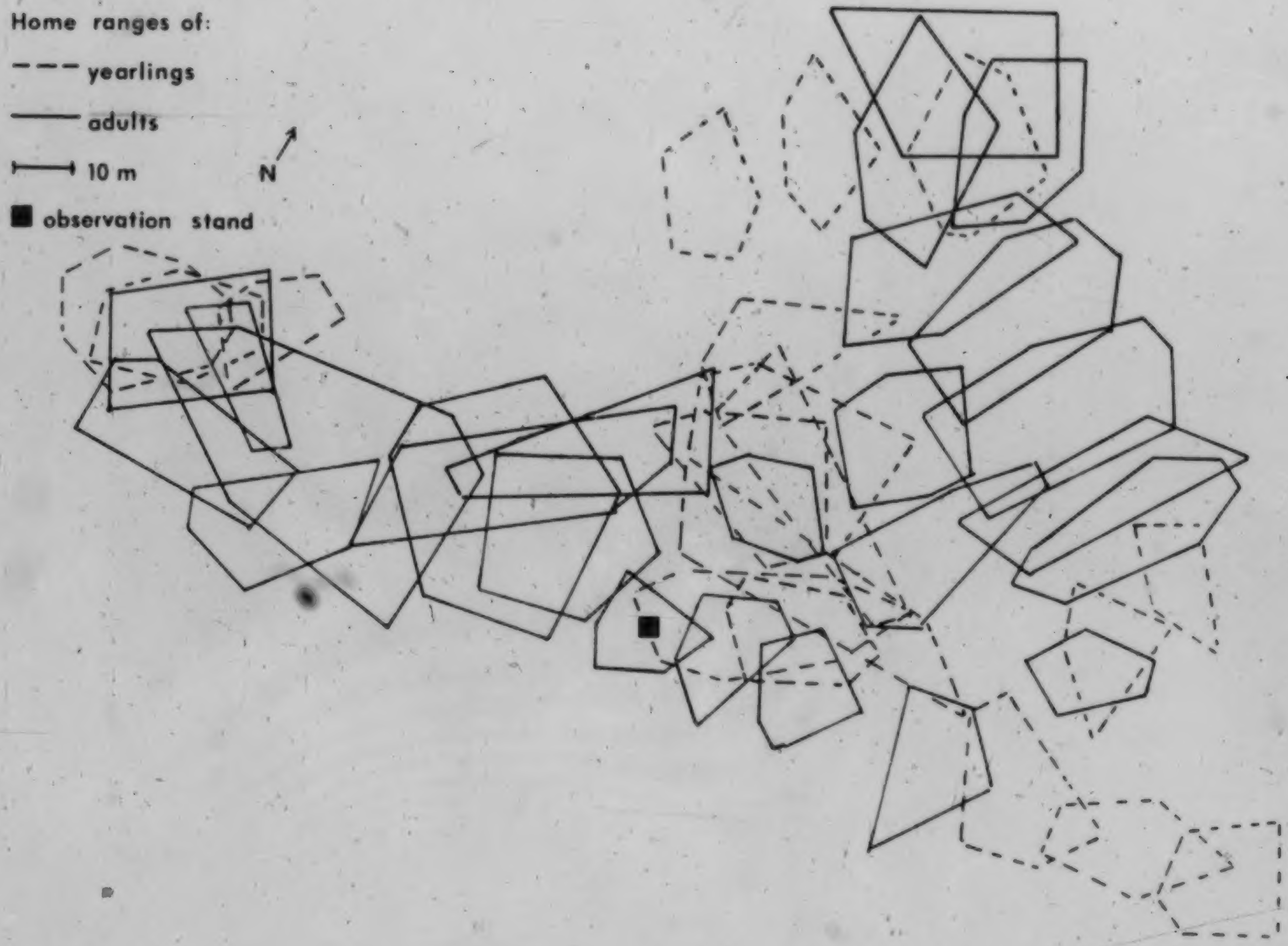
Area = 1275 m^2
n = 13 (8 m, 5 f)
animals/ha = 102

Table 3.2 Mean percent of yearling and adult female home ranges occupied by adult male Columbian ground squirrels during period 3 at NFW, NFE, and RG (1985 and 1986 data combined). Sample sizes in parentheses.

	Mean % home range overlap with:		
Colony	Adult females	Yearlings	Difference[1]
NFW	42.2 (40)	61.3 (37)	$P \leq 0.001$
NFE	32.0 (42)	66.0 (35)	$P \leq 0.001$
RG	55.2 (29)	88.2 (23)	$P \leq 0.001$

[1] Based on Mann-Whitney U-test

Fig. 3.5. Home ranges of adult and yearling Columbian ground squirrels at colony NFE during Period 7, 1986.


Home ranges of:
yearlings
adults
10 m
■ observation stand
N

were widely dispersed over the meadows and overlap between all sex and age classes was extensive, similar to the situation shown in Fig. 3.5.

Yearling communal areas

Yearling communal groups formed every year in each of the three colonies studied. The mean number of yearlings living on a communal area was 10 but ranged from 2-17 animals (Table 3.3). Of the 27 communal groups noted, 22 (81%) were located on areas with hibernacula. The other five areas (3 at NFW, 2 at NFE) were located in areas of low adult female density (eg. the communal area illustrated in the lower right of Fig. 3.2).

Communal areas appeared physically denuded of vegetation presumably because of the high concentrations and activities of adults during the breeding season (Fig. 3.1) and of yearlings during Periods 1-5 (see below). In all but one case communal areas had significantly less vegetative cover than adjacent adult female "territories" (Table 3.4). Forbs and grasses on communal areas were often clipped to the ground by foraging squirrels. As well intensive play behaviour of yearlings on portions of the communal area apparently inhibited vegetative growth. Vegetation on the communal areas matured noticably earlier in hot/dry summers (1984 and 1985) than on adjacent female "territories". Subjectively, the quantity (ie. standing crop biomass) of vegetation per unit area on all female territories appeared much greater than on yearling communal areas.

All yearling males and nonbreeding yearling females lived on communal areas. All 22 yearling females that bred and brought a litter above ground lived away from communal areas in mutually exclusive home ranges elsewhere in the colony. Of the remaining seven yearling females that bred but brought no litter above ground, three lived on a communal area for at least two 10-day intervals while the remaining four lived within the colony but off the communal areas altogether.

In most cases yearlings lived in the same communal area as their littermate siblings. The only exceptions were cases where yearling females bred and lived away from the

Table 3.3 Number of yearling Columbian ground squirrel "communal" groups and mean number of animals per group at colonies NFW, NFE, and RG from 1984-1986.

Colony year	Number of groups	$\bar{x}$ number of animals (group range)	$\bar{x}$ number of littermate subgroups per group (range)
NFW			
1984	5	9.0 (7-13)	-
1985	4	6.8 (2-10)	2.3 (1-3)
1986	7	5.0 (2-14)	1.3 (0-4)
NFE			
1984	2	10.5 (4-17)	-
1985	3	10.0 (9-12)	3.7 (3-4)
1986	3	8.3 (2-14)	2.7 (1-4)
RG			
1984	1	11	-
1985	1	13	5
1986	1	16	6
Weighted Mean	3	10.0	2.6

Table 3.4 Percent vegetative cover on yearling "communal areas" and adult female "territories" at Columbian ground squirrel colonies (NFW, NFE, and RG) in early June, 1985.

Colony	Cover ($\bar{x}$%)			Difference[1]	
	Yearling communal areas (n)		Adult female "territories"	Between communal areas	Between communal areas and territories
	Area 1	Area 2			
NFW	59.7 (20)	55.6 (20)	84.6 (50)	$P > 0.05$	$P \leq 0.001$
NFE	26.7 (20)	62.0 (20)	64.4 (50)	$P \leq 0.001$	$P \leq 0.001$, $P > 0.05$
RG	50.4 (20)	-	80.6 (50)	-	$P \leq 0.001$

[1] Based on Mann-Whitney U-test

communal area (see below). Three juvenile males made home range shifts of greater than 175 m in Period 8 of their first summer and therefore as yearlings lived away from their former natal area and siblings. Thus, communal groups were usually composed of a number of littermate sibling subgroups (Table 3.3).

Although yearlings in communal groups shared a common home area with extensive home range overlap (Figs. 3.3 and 3.4), a degree of differential use of space existed within communal areas. For instance, yearling females usually positioned themselves within a communal area so as to remain close to their mothers' home area even though most yearlings did not have overlapping home ranges with their mother while living on communal areas (see below). Of the 32 yearling females with a surviving mother, 15 (47%) had a nearest adult female neighbour that was not their mother. On average, while female yearlings were living in communal areas (Periods 1 to 5 - see below) mothers ranked as the 1.6th closest adult female neighbour. Yearling males, on the other hand, tended to live farther from their surviving mothers; 50 of 66 (80%) males lived closer to an adult female that was not their mother. Mothers ranked as the 2.5th closest adult female neighbour of yearling males. When brother-sister pairs were compared 57% of males and 39% of females lived closer to an adult female other than their mother (n = 23 sib-pairs). Mothers ranked as the 2.1st nearest adult female neighbour for brothers and the 1.4th closest neighbour for sisters (n = 23 sib-pairs).

The distances between geometric activity centres of yearlings and their mothers were closest during Period 1 (female gestation), increased during Period 2 (late gestation and birth), and remained fairly constant thereafter to Period 5 (late lactation, early juvenile emergence - Table 3.5).

Yearling males lived significantly farther from their mother during Periods 1-5 than did yearling females (Table 3.5). When brother-sister pairs were compared activity centres of sisters were significantly closer to their mothers' activity centre than were the activity centres of brothers during Periods 1-5 (Table 3.6). On average brothers tended to live 8.7 m further from th[illegible] mother than did their sisters.

Table 3.5 Average distance (m) between the activity centres of individual yearling Columbian ground squirrels and their mother's activity centre during Periods 1-5 (data from colonies NFW, NFE, and RG and years 1985 and 1986 combined). Sample sizes in parentheses.

Period	Yearling		Difference[2]
	Male	Female[1]	
1	28.9 (65)	14.5 (33)	$P \leq 0.01$
2	46.4 (67)	31.0 (32)	$P \leq 0.05$
3	46.9 (66)	27.4 (32)	$P \leq 0.01$
4	47.5 (66)	26.6 (32)	$P \leq 0.001$
5	51.7 (63)	33.2 (31)	$P \leq 0.01$

[1] Excludes females that bred

[2] Based on Mann-Whitney U-test

Table 3.6 Average distance (m) of the activity centres of yearling brothers and sisters from their mother's activity centre during Periods 1-5 (data from colonies NFW, NFE, and RG; 1985-1986 combined, n = 23 sibling pairs).

Period	Sister[1]	Brother	Difference[2]
1	13.7	18.8	$P \leq 0.01$
2	16.3	21.4	$P \leq 0.001$
3	17.2	28.8	$P \leq 0.001$
4	16.0	24.8	$P \leq 0.001$
5	20.3	33.0	$P \leq 0.001$

[1] Excludes sisters that bred

[2] Based on Wilcoxon-paired sample test

The differences noted in distance from the mother's centroid for yearling males and females (and brother-sister pairs) was also reflected in the percent overlap in the home ranges of yearlings and their mother (Tables 3.7 and 3.8). During Period 1 there was no difference between yearlings (male vs females, brother vs sister pairs) in the amount of overlap with the mother but during Periods 2-5 male yearlings had much less overlap with their mother than did female yearlings (Table 3.7). During Periods 2-5 40 of 66 (61%) yearling males shared no part of their home range with their mother whereas this was true of only 8 of 25 (32%) yearling females. Both yearling males and females had the least amount of home range overlap with their mother during Period 3 (female parturition/early lactation) and Period 5 (late lactation/early juvenile emergence - Tables 3.7 and 3.8).

Yearling home ranges overlapped those of adult males to a considerable degree during Periods 1-5, as expected from the distribution of yearling and adult males within the colonies (Table 3.9 and Fig. 3.2). For both yearling males and females home range overlap with adult males slowly declined from high levels in Period 1 to relatively low levels in Period 5 (Table 3.9). This resulted mostly from the slow attrition in home range size of adult males over Periods 1 to 5 (Appendix 11) and to home range shifts of yearlings away from the communal area beginning in Periods 4 and 5 (see below). Adult male home ranges overlapped significantly more with the ranges of yearling females than with the ranges of yearling males in Periods 1, 4, and 5. Yearling males tended to avoid encounters with adult males during Periods 4 and 5 whereas yearling females showed no such avoidance behaviour (Chapter 6). These differences in avoidance behaviour may have resulted in the differences observed in the home range overlap values of yearling males and females with adult males.

To summarize, all yearling males and nonbreeding yearling females lived on "communal" areas with other yearlings and with some adult males. Yearling home ranges overlapped extensively with other yearling and adult male home ranges. Siblings almost always lived together in the same communal group but also were associated with other less closely related yearlings. Female yearlings tended to position themselves closer to and overlapped

Table 3.7 Average percent home range overlap between yearling Columbian ground squirrels and their mothers during Periods 1-5 (data from colonies NFW, NFE, and RG and years 1985 and 1986 combined). Sample sizes in parentheses.

Period	Yearlings		Difference[2]
	Male	Female[1]	
1	35.2 (65)	33.4 (33)	$P > 0.05$
2	13.7 (67)	33.5 (32)	$P \leq 0.01$
3	9.8 (66)	25.4 (32)	$P \leq 0.01$
4	15.3 (66)	37.1 (32)	$P \leq 0.01$
5	9.6 (63)	27.1 (31)	$P \leq 0.01$

[1] Excludes females that bred

[2] Based on Mann-Whitney U-test

Table 3.8 Average percent home range overlap of brothers and sisters with their mother during Periods 1-5 (data from colonies NFW, NFE, and RG, 1985 and 1986 combined, n = 23 sibling pairs).

Period	Brother	Sister[1]	Difference[2]
1	26.3	29.6	$P > 0.05$
2	24.6	38.1	$P \leq 0.001$
3	15.3	23.7	$P \leq 0.01$
4	24.3	35.6	$P \leq 0.001$
5	18.0	30.7	$P \leq 0.001$

[1] Excludes sisters that bred

[2] Based on Wilcoxon-paired sample test

Table 3.9 Average percent overlap between the home ranges of yearling and adult male Columbian ground squirrels during Periods 1-5. (Data from colonies NFW, NFE, and RG and years 1985 and 1986 combined). Sample sizes in parentheses.

	Yearlings		
Period	Male	Female[1]	Difference[2]
1	68.5 (96)	80.0 (40)	$P \leq 0.05$
2	66.0 (96)	70.5 (39)	$P > 0.05$
3	69.1 (95)	62.7 (39)	$P > 0.05$
4	48.6 (95)	57.2 (39)	$P \leq 0.05$
5	38.8 (92)	51.9 (38)	$P \leq 0.05$

[1] Excludes females that bred

[2] Based on Mann-Whitney U-test

more with their mothers than did male yearlings but a yearling female's mother was still not always her closest neighbour.

The spatial history of individuals

During the first 2-5 days above ground juveniles rarely were sighted more than 10 m from the natal burrow. Only 2 of 111 juveniles (2%), both males, shifted their activity centres by more than one home range diameter (HRD - see Appendix 7) during the first 20 to 30 days above ground (Periods 5-7 - Fig. 3.6). On average, during Periods 5-7, juvenile activity centres were 8.1 and 6.4 m from the natal burrow and 7.7 and 7.0 m from their mother's activity centre for males and females respectively (Figs. 3.7, 3.8, 3.9 and 3.10).

Later on, during Periods 8-10, 14 of 130 juveniles (11%) shifted their activity centres by one or more HRD's (Fig. 3.6). At NFW, during Periods 8-10 in 1985, three juvenile males moved to new activity centres 175, 240, and 313 m from their natal burrows. These three home range shifts greatly exaggerated the mean distance from the natal burrow recorded for juvenile males during Periods 8-10 at NFW (Fig. 3.7). When these three long-distance home range shifts were excluded, juvenile males at NFW in 1985 lived an average of 11.7 m (range 3.0-39.2 m) from the natal burrow compared to the 50.2 m average recorded when all home range shifts were included (Fig. 3.7). Activity centres of juveniles during Periods 8-10 for all colonies combined (but excluding these three long-distance shifts) were 16.0 and 17.3 m from the natal burrow and 10.8 and 10.0 m from the mother's activity centre for males and females respectively.

Prior to immergence juveniles were often seen moving onto "common" areas of hibernacula (see description Appendix 10) away from their previous home ranges. These shifts in activity usually were late in Period 10 and later after regular observations had stopped, and thus did not become evident in the data until the following season when the animals emerged from hibernation as yearlings in Periods E and 1. In total, 33 of 126 juveniles (26%) emerged the following spring one or more HRD's away from their juvenile activity centre during

Fig. 3.6. Proportion of Columbian ground squirrels shifting activity centre by distances greater than or equal to one home range diameter (HRD) during their juvenile, yearling, and adult lives. Data are pooled for the 1983, 1984, and 1985 cohorts at NFW, NFE, and RG. Sample sizes for each sex are given above each time period. Yearling females that bred were excluded.

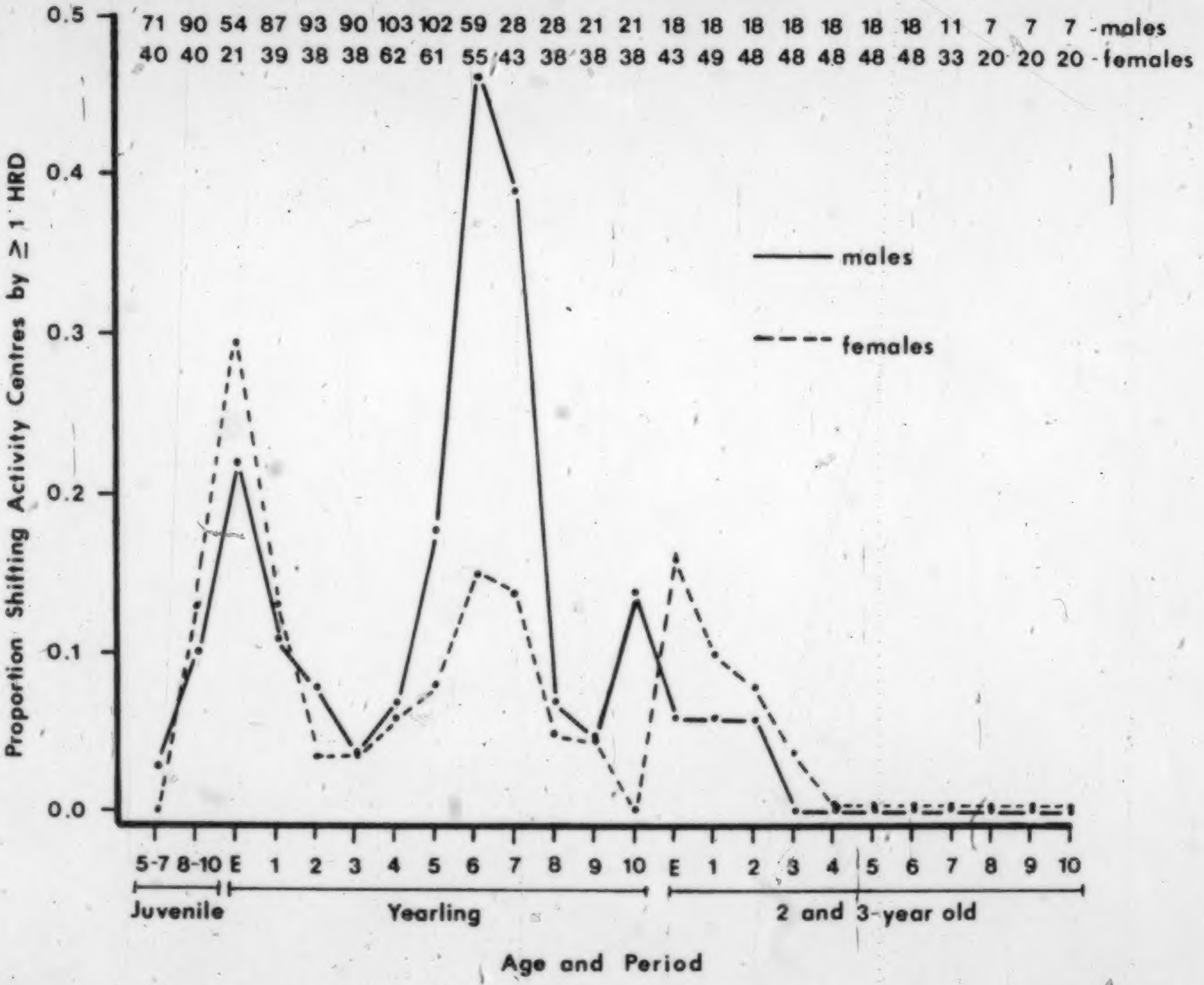

71 90 54 87 93 90 103 102 59 28 28 21 21 18 18 18 18 18 18 18 11 7 7 7 - males
40 40 21 39 38 38 62 61 55 43 38 38 38 43 49 48 48 48 48 48 33 20 20 20 - females
0.5
0.4
0.3
0.2
0.1
0.0
Proportion Shifting Activity Centres by ≥ 1 HRD
males
females
5-7
8-10
E
1
2
3
4
5
6
7
8
9
10
E
1
2
3
4
5
6
7
8
9
10
Juvenile
Yearling
2 and 3-year old
Age and Period

Fig. 3.7. Mean distance (m) of the activity centre of male Columbian ground squirrels from their natal burrows over time for individuals of the 1984 and 1985 juvenile cohort at colonies NFW, NFE, and RG. Sample sizes are given above each time period.

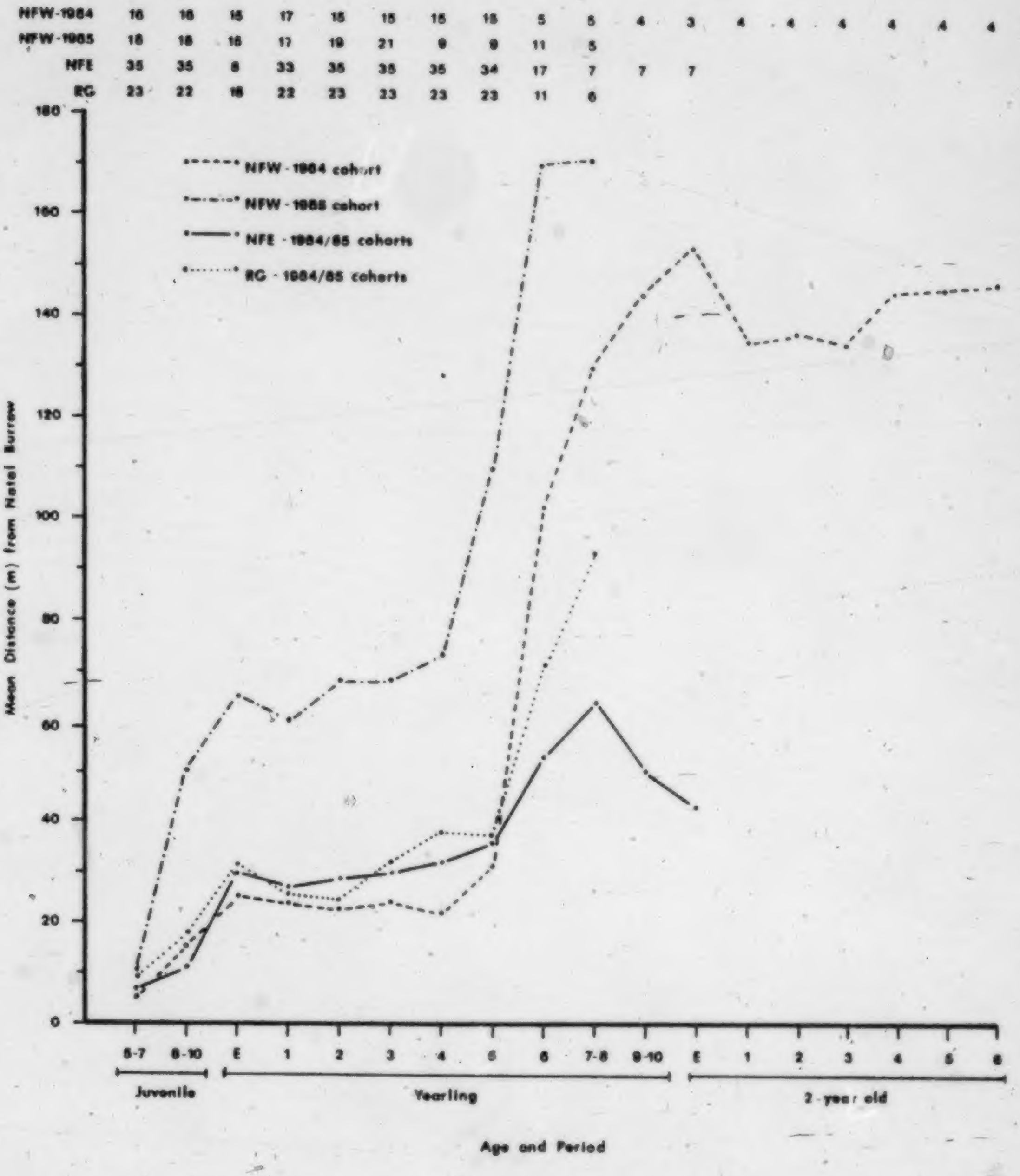

NFW-1984 16 18 15 17 15 15 15 15 5 5 4 3 4 4 4 4 4 4
NFW-1985 18 18 16 17 19 21 9 9 11 5
NFE 35 35 8 33 35 35 35 34 17 7 7 7
RG 23 22 18 22 23 23 23 23 11 6
NFW - 1984 cohort
NFW - 1985 cohort
NFE - 1984/85 cohorts
RG - 1984/85 cohorts
Mean Distance (m) from Natal Burrow
0
20
40
60
80
100
120
140
160
180
5-7
8-10
E
1
2
3
4
5
6
7-8
9-10
E
1
2
3
4
5
6
Juvenile
Yearling
2-year old
Age and Period

Fig. 3.8. Mean distance (m) of the activity centre of female Columbian ground squirrels from their natal burrows over time for individuals of the 1984 and 1985 juvenile cohorts at colonies NFW, NFE, and RG. Sample sizes are given above each time period. Excludes females that bred as yearlings.

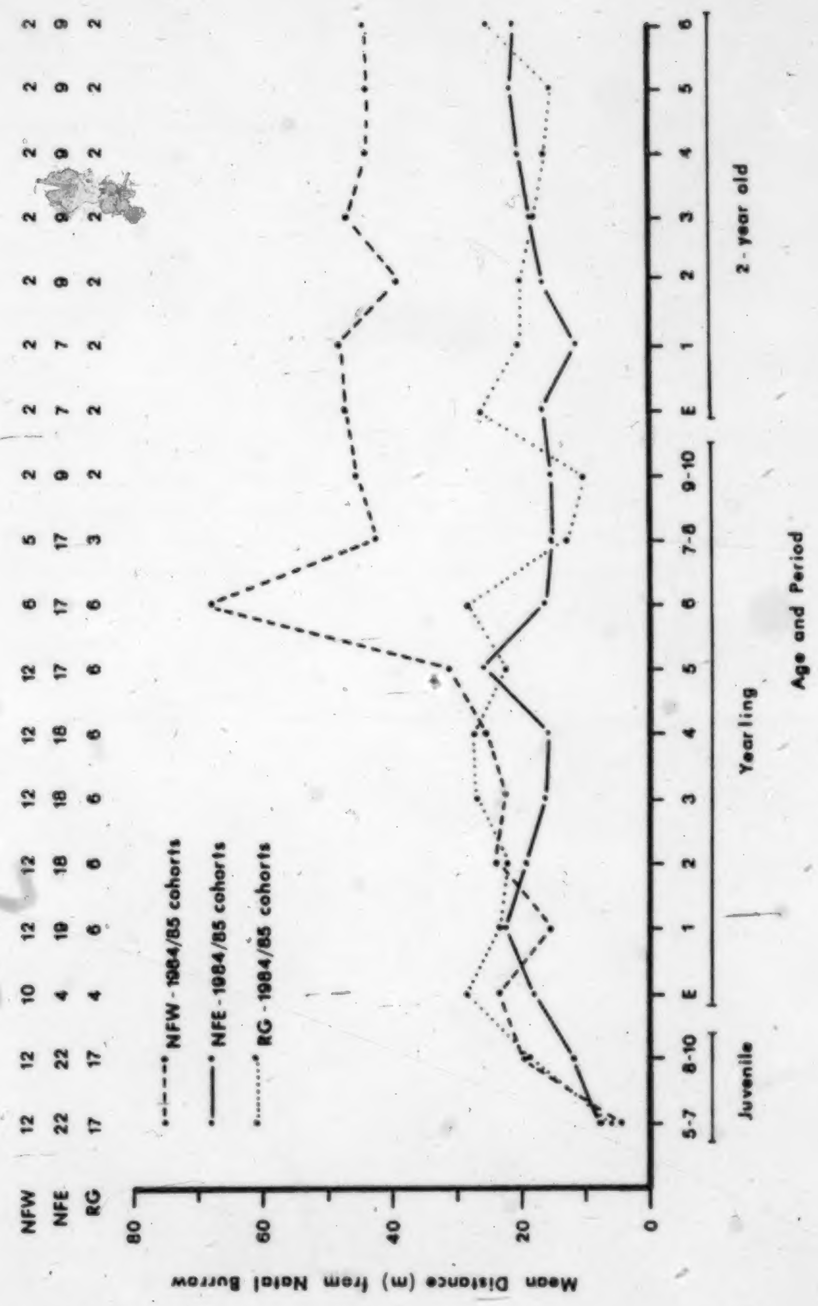

NFW 12 12 10 12 12 12 12 12 6 5 2 2 2 2 2 2 2 2
NFE 22 22 4 19 18 18 18 17 17 17 9 7 7 9 9 9 9 9
RG 17 17 4 6 6 6 6 6 6 3 2 2 2 2 2 2 2 2
NFW - 1984/85 cohorts
NFE - 1984/85 cohorts
RG - 1984/85 cohorts
Mean Distance (m) from Natal Burrow
80
60
40
20
0
5-7
8-10
E
1
2
3
4
5
6
7-8
9-10
E
1
2
3
4
5
6
Juvenile
Yearling
2 - year old
Age and Period

Fig. 3.9. Mean distance of the activity centre of male Columbian ground squirrels from their mothers' activity centres for individuals of the 1984 and 1985 juvenile cohorts at colonies NFW, NFE, and RG. Sample sizes are given above each time period.

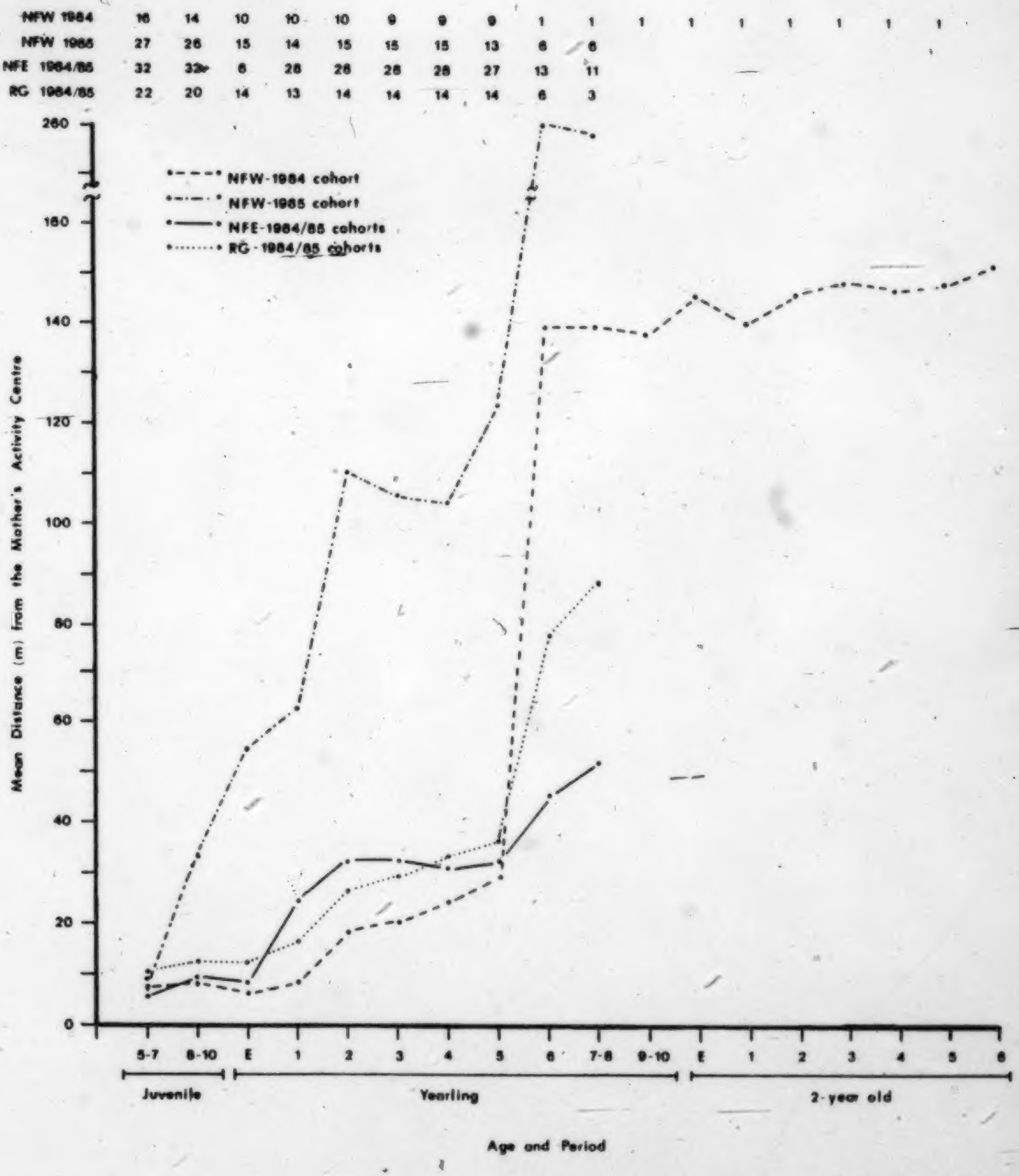
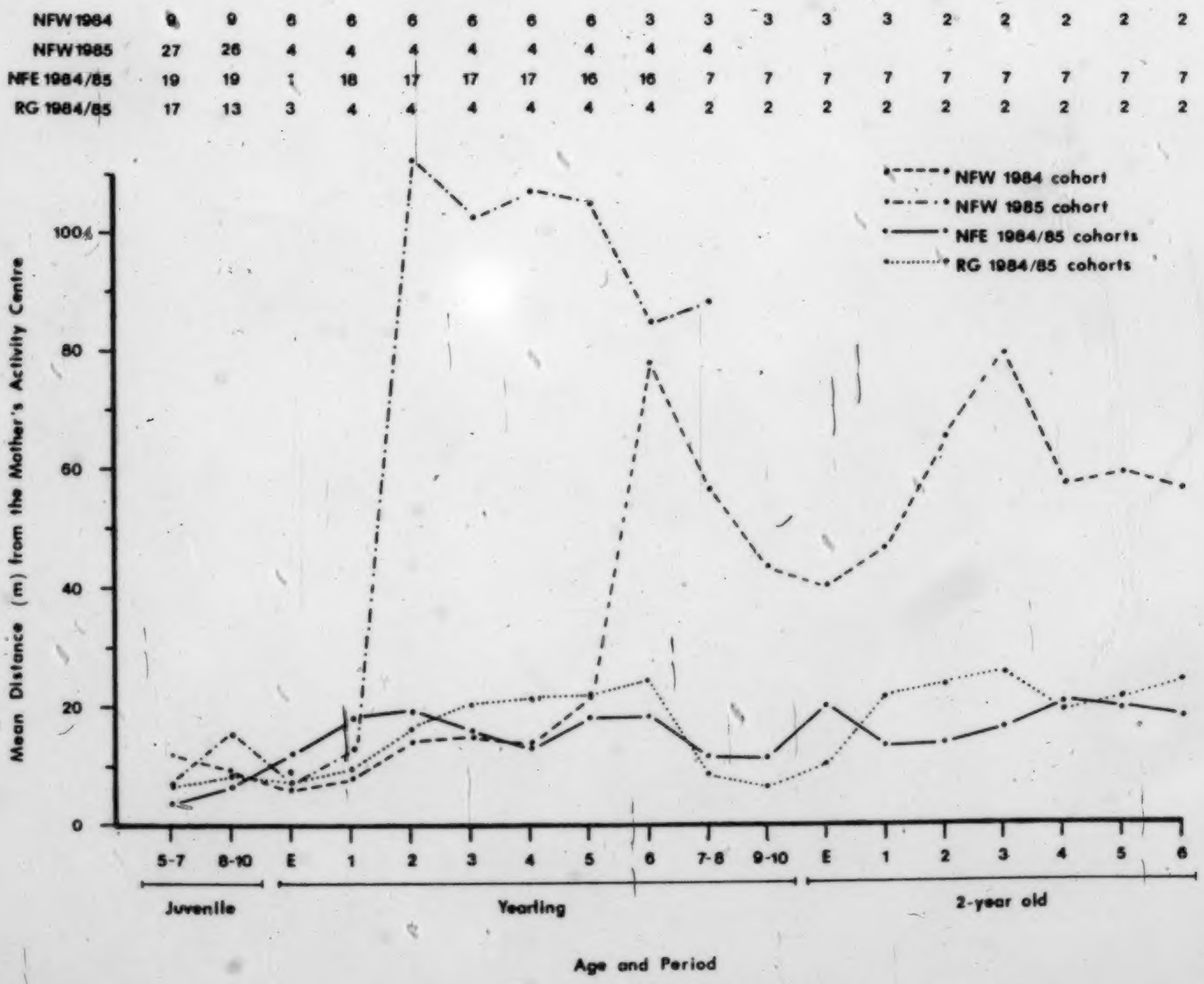

NFW 1984 16 14 10 10 10 9 9 9 1 1 1 1 1 1 1 1 1
NFW 1985 27 26 15 14 15 15 15 13 6 6
NFE 1984/85 32 32 8 28 28 28 28 27 13 11
RG 1984/85 22 20 14 13 14 14 14 14 6 3
NFW-1984 cohort
NFW-1985 cohort
NFE-1984/85 cohorts
RG-1984/85 cohorts
260
160
140
120
100
80
60
40
20
0
Mean Distance (m) from the Mother's Activity Centre
5-7
8-10
E
1
2
3
4
5
6
7-8
9-10
E
1
2
3
4
5
6
Juvenile
Yearling
2-year old
Age and Period

Fig. 3.10. Mean distance of the activity centre of female Columbian ground squirrels from their mothers' activity centre for individuals of the 1984 and 1985 juvenile cohorts at colonies NFW, NFE, and RG. Sample sizes are given above each time period. Excludes females that bred as yearlings.


NFW 1984 9 9 6 6 6 6 6 6 3 3 3 3 3 2 2 2 2 2
NFW 1985 27 26 4 4 4 4 4 4 4 4
NFE 1984/85 19 19 1 18 17 17 17 16 16 7 7 7 7 7 7 7 7 7
RG 1984/85 17 13 3 4 4 4 4 4 4 2 2 2 2 2 2 2 2 2
NFW 1984 cohort
NFW 1985 cohort
NFE 1984/85 cohorts
RG 1984/85 cohorts
Mean Distance (m) from the Mother's Activity Centre
100
80
60
40
20
0
5-7
8-10
E
1
2
3
4
5
6
7-8
9-10
E
1
2
3
4
5
6
Juvenile
Yearling
2-year old
Age and Period

Periods 8-10 (Fig 3.6). The average shift in activity centre during this time was 23.9 m (range 1-112 m) for males and 19.8 m (range 1-80 m) for females (Figs. 3.7 and 3.8).

Adult females and their offspring overwintered in close proximity; the distance between activity centres of yearlings and their mothers at emergence was only 9.0 m for males and 8.7 m for females (Figs. 3.9 and 3.10). At NFW the three juveniles that had shifted their home ranges by long distances during Periods 8-10 in 1985, emerged the following spring in the region where they had lived as juveniles in Periods 8-10. Thus as yearlings they lived at a great distance from their natal burrow and mother which greatly exaggerated the mean recorded for males of the 1985 cohort at NFW (Figs. 3.7 and 3.9). When these three males were excluded from the analysis yearlings of the 1985 cohort at NFW lived on average 20.5 m from their natal burrow and 7.7 m from their mothers' activity centre during Period E. These numbers are similar to the distances recorded for males of the NFW 1984 cohort and the NFE and RG cohorts (Figs. 3.7 and 3.9).

During Periods 1 and 2 (gestation) adult females moved away from the areas that they occupied at emergence and returned to the areas they had occupied the previous season (see below). The movement of females away from areas of hibernacula resulted in increased distances between mother and offspring (Figs. 3.9 and 3.10). By Period 3 (parturition/early lactation) mothers lived an average of 29.5 m from their yearling sons and 16.5 m from their yearling daughters (Figs. 3.9 and 3.10 - excluding yearling males and females from the NFW 1985 cohort). The mean distance recorded between mothers and their yearling sons during Period 3 for the NFW 1985 cohort was inflated relative to the mean recorded for the NFW, NFE and RG (1984) cohorts because of the three long-distance home range shifts of the three males previously discussed. As well, three adult females that had four yearling sons present shifted their activity centres in Period 2 by 94, 180, and 165 m. These three shifts further inflated the mean distance recorded between sons and mothers (Fig. 3.9). When these six long-distance shifts were excluded the mean distance that yearling males of the NFW 1985 cohort lived from their mothers activity centre dropped from 110.3 m to 38.6 m - similar to the average distance recorded for the cohorts at other colonies and years (Fig. 3.9). The high mean distance recorded between mother and yearling female offspring at NFW (1985 cohort) during and after Period 2 was also a result of the long-distance movements of the three mothers (Fig. 3.10). For all colonies and years combined (excluding the above-mentioned long-distance movements) yearling male and female activity centres were 31.2 and 16.1 m from their mother's activity centres during Period 3, a difference that was significant (Mann-Whitney U test, $P \leq 0.001$).

From the time of emergence in Periods E and 1 until Periods 4 or 5, nonbreeding yearlings of both sexes lived on communal areas that often coincided with the areas where the squirrels emerged from hibernation (Appendix 10). Once yearlings emerged they remained relatively sedentary while in the communal areas. Few yearlings (10% of males and 6% of females) shifted their activity centres by greater than 1 HRD during Periods 1-4. The average change in distance of activity centres between 10-day periods during Periods 1-4 was 10.5 m for males and 10.6 m for females. As such, the mean distance of yearlings from the natal burrow while living on communal areas remained relatively constant over time until Period 5 when squirrels began to shift home ranges away from the communal area (see below). On average, yearling males (excluding the three long-distance movements recorded from the NFW 1985 cohort) lived significantly farther(Mann-Whitney U Test, $P \leq 0.01$). from their natal burrow (31.6 m) during Periods E to 4 than yearling females (20.3 m). The distance that yearling activity centres were from their natal burrows and their mothers' activity centres during tenure on communal areas (Periods E to 4) were very similar (distance from natal burrows and mothers' activity centres were 31.6 and 31.2 m, respectively, for males and 20.3 and 16.2 m, respectively, for females) suggesting that the mothers returned to the nest site of the previous year.

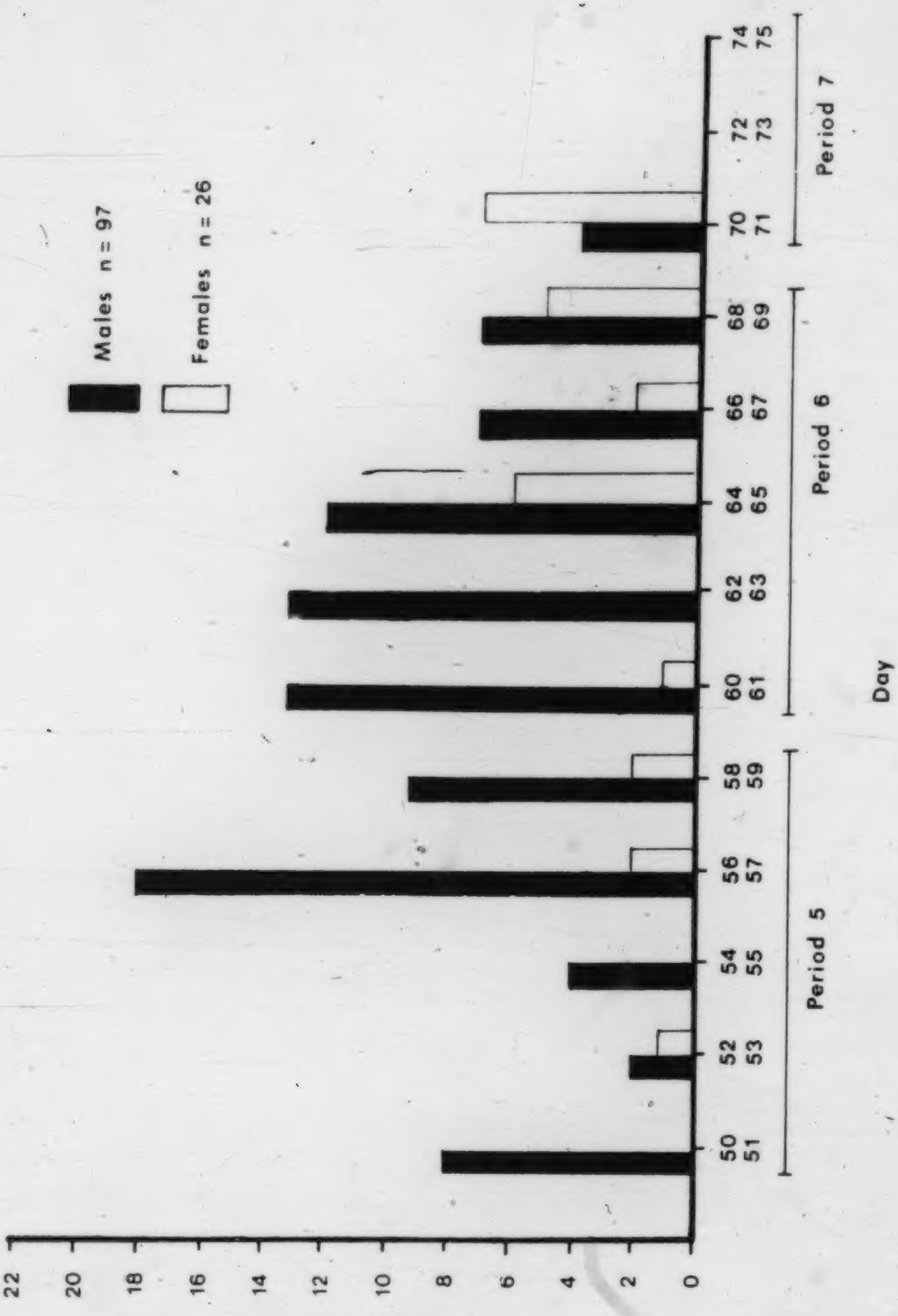
The proportion of yearlings shifting activity centres by one or more HRD's increased in Period 5, and peaked during Periods 6 and 7 (Fig. 3.6). During these three periods significantly more males (30%) than females (11%) shifted activity centres by one or more

HRDs ($\chi^2=4.34$; $P\leq0.05$ - Fig. 3.6). These proportions represent only those shifts in activity centre that occurred within the confines of the natal colony; intercolony movements were not included. During Periods 5 and 6, 101 of the 139 yearling males present in 1984-1986 were known either to have dispersed (18 animals) or presumed to have dispersed (83 animals) from their natal colony (Table 3.1, Fig. 3.11 and Chapter 2). In total, including all intracolony and intercolony movements, 131 of 139 (94%) male yearlings shifted or presumably shifted their activity centres by one or more HRDs during Periods 5, 6 or 7. Among females, 28 yearlings were known either to have dispersed (6 animals) or presumed to have dispersed (22 animals) from their natal colony and these losses also occurred mostly during periods 5 and 6 (Fig. 3.11). Of the 45 nonbreeding yearling females remaining in the natal colony 11 (or 24%) shifted activity centres sometime during periods 5, 6 and 7. In total 39 of the 73 (53%) nonbreeding female yearlings present in these colonies shifted their activity centres by one or more HRDs during Periods 5, 6 or 7.

Among male yearlings the distance from their natal burrows and from their mothers' activity centres increased greatly during Period 6 and remained high at this distance during Periods 7 and 8 and for all periods recorded thereafter (Figs. 3.7 and 3.9). The mean distance of yearling male activity centres from their natal burrows and their mothers' activity centres during Periods 7-8 varied for each of the cohorts followed but averaged 109.0 and 120.1 m respectively (Figs. 3.7 and 3.10). Since these measures only included intracolony shifts in activity centres, the differences in mean distances recorded between the three colonies were probably related to differences in the physical size of each colony. In the largest colony, NFW, there was greater opportunity for animals to shift their activity centres over longer distances than was possible in the two smaller colonies, NFE and RG (see Appendix 9 for details of colony size).

Although a number of yearling females (11 of the 45 that remained in the natal colony) shifted home range during Periods 6 and 7, the mean distance that they resided from their natal burrows remained small. During Periods 7-8 at NFE and RG, yearling female

Fig. 3.11. Time last sighted by 2-day periods for yearling male and female Columbian ground squirrels that dispersed or presumably dispersed from their natal colony. Data are from colonies NFW, NFE, and RG, 1984-1986.



Males n = 97
Females n = 26
Number of Animals
22
20
18
16
14
12
10
8
6
4
2
0
50 51
52 53
54 55
56 57
58 59
60 61
62 63
64 65
66 67
68 69
70 71
72 73
74 75
Period 5
Period 6
Period 7
Day

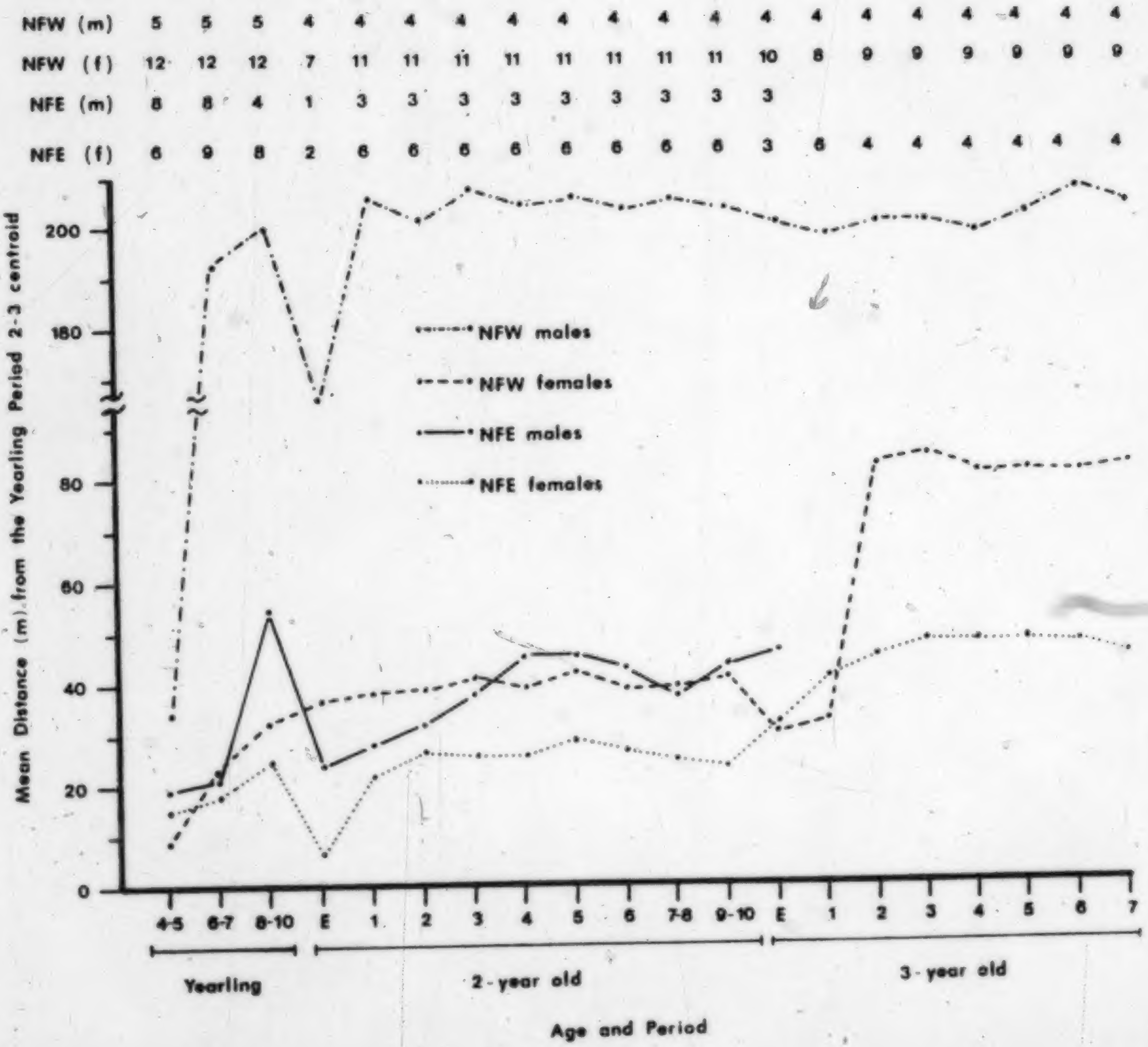
activity centres were only 15.2 m from their natal burrows - closer than recorded during these same female's tenure on communal areas (Fig. 3.8). Apparently home range shifts for females at NFE and RG during Periods 6 and 7 were towards the natal site rather than away from it as noted previously for males.

At NFW yearling females seemed to move away from the natal burrow during Period 6 but towards it during periods 7-8 (Fig. 3.8). Three of the six nonbreeding yearling females for which information was available had their activity centres >100 m from their natal burrows during Period 6 (x = 112.1 m). The other three females lived an average of 32.3 m from their natal burrows during this time. One of the females that lived more than 100 m from its natal burrow dispersed late in Period 6. In Periods 7-8 another female that had lived >100 m from its natal burrow, shifted its activity centre back to within 33 m of its natal burrow. That left one female with an activity centre 111.6 m from its natal burrow and four others with centres on average 25.0 m from their natal burrows.

For individuals of the 1983 cohort, first studied as yearlings in 1984, the distances that their activity centres were from their activity centres of Periods 2-3 (representative of the communal area) were measured over time (Fig. 3.12). Great shifts in activity centres occurred during periods 6-7 for males at NFW which lived an average of 192.3 m from the activity centres they occupied during Periods 2-3.

The proportion of 2- and 3-year olds that shifted home range by one or more HRDs was small relative to the proportions noted for yearlings. On average fewer than 4% of 2 and 3-year olds shifted activity centres by more than one HRD during the course of the active season (Fig. 3.6). Most home range shifts by 2- and 3-year olds were associated with movements onto or off of hibernacula areas at immergence and emergence. As well, home range shifts of four 3-year-old females (two at NFW, two at NFE) during Periods 1 and 2 were apparently the result of relinquishment of the natal site to their reproductively active yearling daughters (see below and Appendix 12).

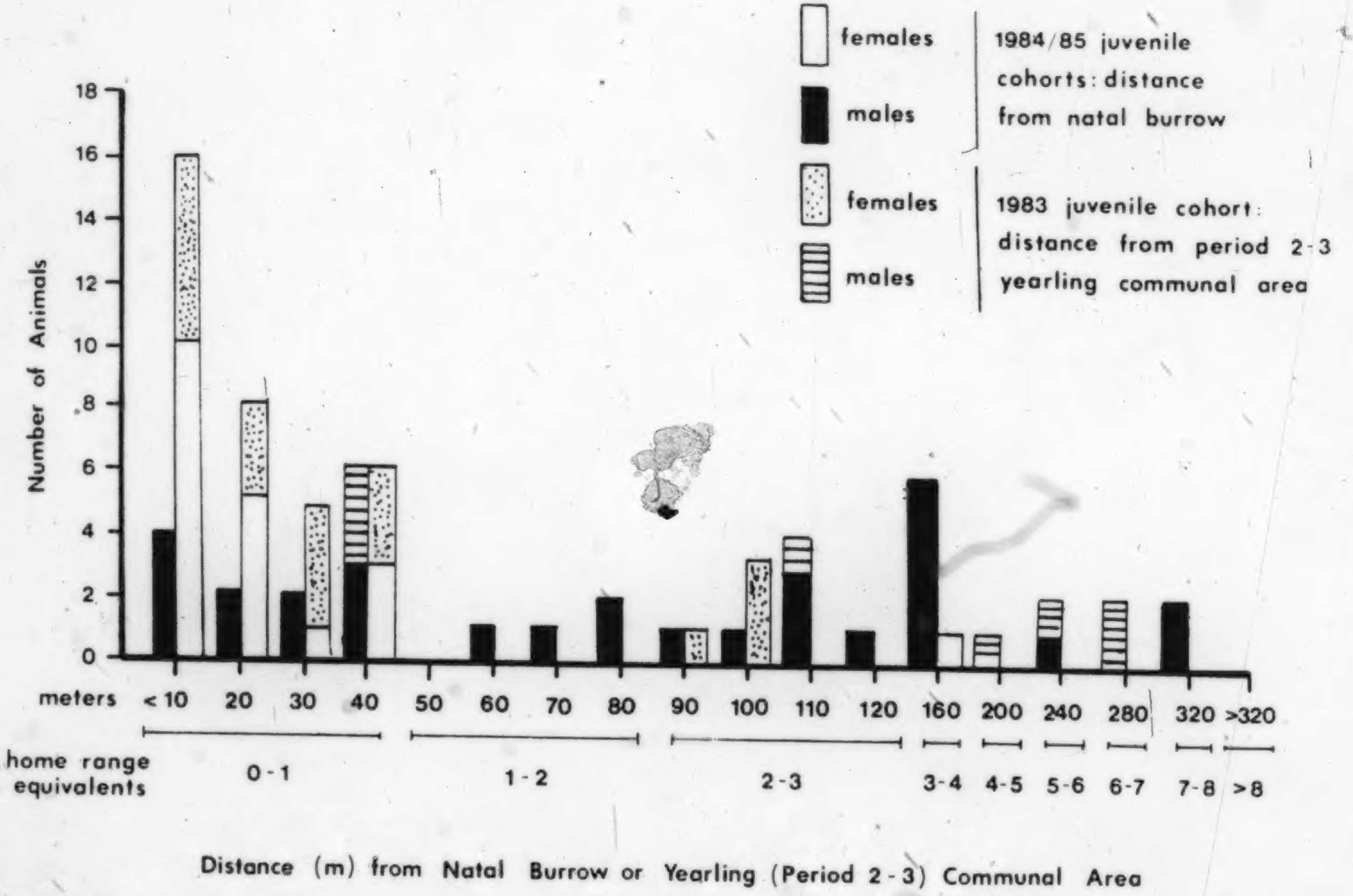
Fig. 3.12. Mean distance (m) from the activity centres (centroids) of yearlings during Periods 2-3 for individuals of the 1984 yearling cohort at colonies NFW and NFE. Sample sizes for each sex are given above the time periods. Excludes females that bred as yearlings.


NFW (m) 5 5 5 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4
NFW (f) 12 12 12 7 11 11 11 11 11 11 11 11 10 8 9 9 9 9 9 9
NFE (m) 8 8 4 1 3 3 3 3 3 3 3 3 3
NFE (f) 6 9 8 2 6 6 6 6 6 6 6 6 3 6 4 4 4 4 4 4
Mean Distance (m) from the Yearling Period 2-3 centroid
200
180
80
60
40
20
0
NFW males
NFW females
NFE males
NFE females
4-5
6-7
8-10
E
1
2
3
4
5
6
7-8
9-10
E
1
2
3
4
5
6
7
Yearling
2-year old
3-year old
Age and Period

Beginning during Periods 7-8 of the ~~yearling~~ active season through to ages 2 and 3 years, there was relatively little change in the mean distance that individual activity centres were from their natal burrows (Figs. 3.7 and 3.8) or from the activity centres of yearling Periods 2-3 (Fig. 3.12). Apparently the areas where yearlings resided late in their yearling active seasons (eg. Periods 7-8) were the areas where they eventually settled and bred as adults (at least at age 3). The only large shifts in activity centres noted for 2- or 3-year-old individuals was for the four females that relinquished their home areas to their yearling daughters (Appendix 12). At NFW both such home range shifts (325 and 150 m) occurred during Period 2 while at NFE the shifts (80 and 125 m) occurred during periods 1 and 2. Thus females moved to a new site before giving birth to the new litter. These four movements inflated the average recorded for all females at NFW and NFE, but all remaining females continued to live in the same areas at a relatively constant distance activity centres occupied during Periods 2-3 as yearlings (Fig. 3.12).

The centroid occupied by yearlings during Periods 7-8 was considered to be representative of the area where these squirrels eventually settled (Figs. 3.7, 3.8 and 3.12). The distribution of the distances moved from the natal burrow for the 1984 and 1985 cohorts or from the centroid occupied during Periods 2-3 for the 1983 cohort are outlined in Fig. 3.13. Few females (5/40 = 12%) that remained in the natal colony lived more than 40 m (one adult male home range equivalent) from their natal burrows or yearling communal area. Of yearling males that remained in the natal colony, 63% (24/38) lived more than one home range diameter (40 m) from their natal site or yearling communal area. Had intercolony dispersers (Table 3.3 and Chapter 2) been included the percentage of animals that were known to have lived or presumed to have lived more than one adult male home range diameter from the natal burrow (or communal area) increased to 90% (125/139) for males and 44% (32/73) for females. Of the 14 males that remained within 40 m of their natal or communal area, 12 were from NFE (3 in 1984, 4 in 1985 and 5 in 1986), one was from RG, and the remaining one was from NFW.

Fig. 3.13. Distance from the natal burrow or the activity centre occupied during Periods 2-3 as yearlings at which Columbian ground squirrels from the 1983-1985 juvenile cohorts at colonies NFW, NFE, and RG settled as yearlings in Periods 7-8, excluding females that bred as yearlings.

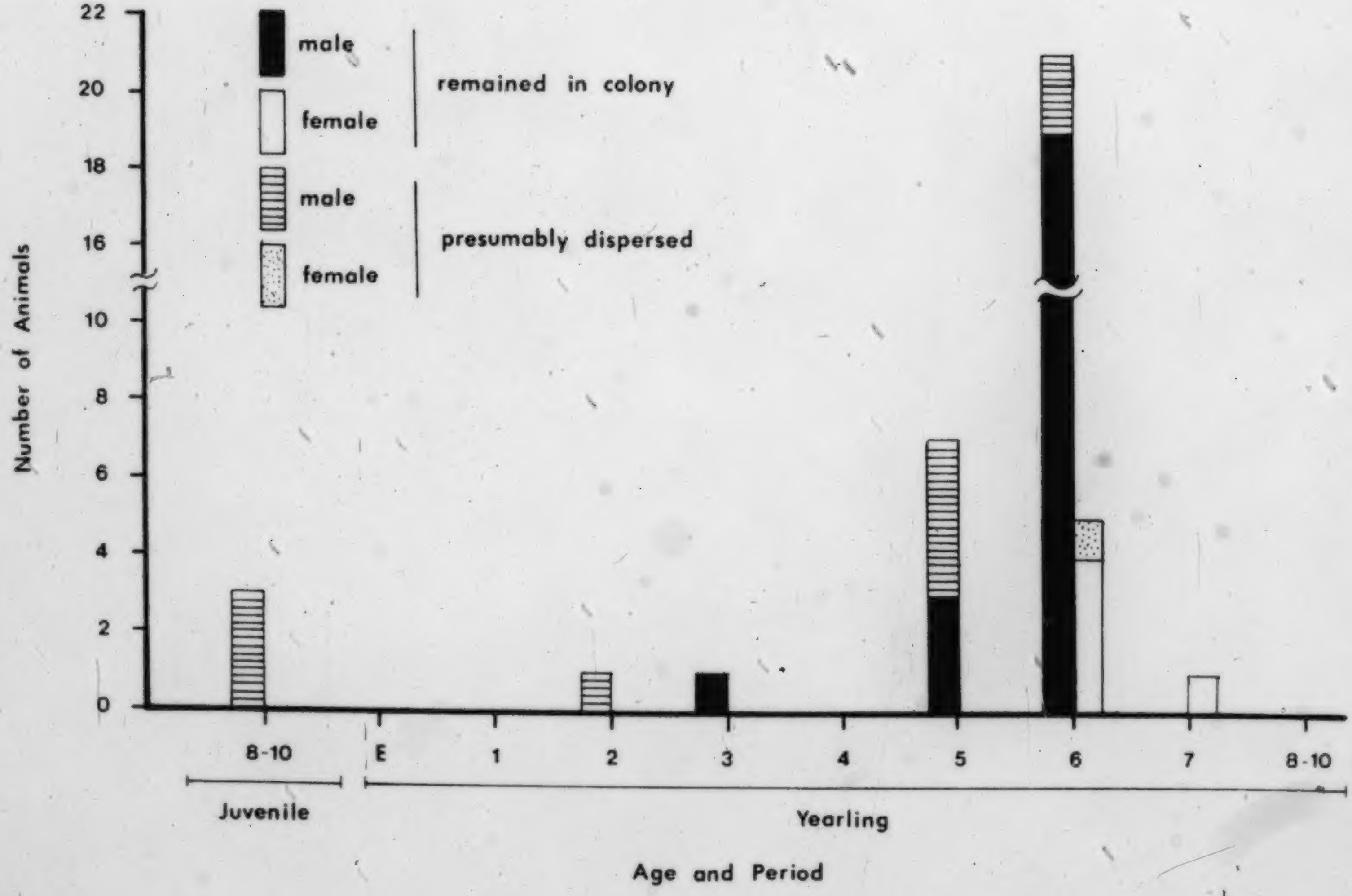

Number of Animals
18
16
14
12
10
8
6
4
2
0
females
males
1984/85 juvenile cohorts: distance from natal burrow
females
males
1983 juvenile cohort: distance from period 2-3 yearling communal area
meters
< 10
20
30
40
50
60
70
80
90
100
110
120
160
200
240
280
320
>320
home range equivalents
0 - 1
1 - 2
2 - 3
3 - 4
4 - 5
5 - 6
6 - 7
7 - 8
> 8
Distance (m) from Natal Burrow or Yearling (Period 2 - 3) Communal Area

All animals that moved 40 m or less retained essentially the same adult neighbours as they had prior to their move. On the other hand, all animals that moved by 80 m or more (two or more home range equivalents) lived spatially isolated from their former neighbours (at least in terms of their 80% core areas). Of the four males that moved between 41 to 80 m (Fig. 3.13), two that moved 58 and 61 m continued to live associated with at least one former adult neighbour whereas the other two (both males) that moved 72 and 79 m lived away from their former spatial associates. Thus all movements of yearlings to their final place of settlement could be classified into two categories, those establishing 1) away from and 2) among former adult neighbours.

Of the 22 males that moved away from the vicinity of their adult neighbours but remained within the confines of their natal colony, 21 (96%) moved during Periods 5 and 6 (Fig. 3.14). Nearly all known and presumed intercolony dispersal also occurred during Periods 5 and 6 (Fig. 3.12). Thus the vast majority of shifts away from the vicinity of adult neighbours occurred during Periods 5 and 6. One male shifted its activity centre to the area where it finally settled during Period 3. The three juveniles that shifted their activity centres by >100 m in Periods 8-10 (Fig 3.14) later disappeared (presumably dispersed) during early Period 6 as yearlings. Seven other yearling males and one yearling female also shifted activity centres away from the vicinity of their neighbours before finally disappearing during Periods 5 and 6. Seven of these eight shifts occurred during Periods 5 and 6; the remaining animal, a male, moved away from the vicinity of its adult neighbours during Period 2. Of the five females recorded shifting their activity centres by more than 80m, four moved during Period 6, and one left during Period 7. Thus the majority of intracolony and intercolony "home range shifts" occurred during Periods 5 and 6 but a few intracolony "shifts" were recorded during earlier periods both by juveniles and as yearlings.

The number of home range vacancies that yearlings traversed before settling was compared for males and females. Vacancies were defined as areas unoccupied in the spring that were occupied later by immigrants (either inter- or intracolony immigrants). The number

Fig. 3.14. Periods when male and female Columbian ground squirrels shifted activity centres away from the vicinity of their adult neighbours. Excludes female yearlings that bred.


Number of Animals
22
20
18
16
10
8
6
4
2
0
male
female
remained in colony
male
female
presumably dispersed
8-10
E
1
2
3
4
5
6
7
8-10
Juvenile
Yearling
Age and Period

of vacancies traversed before settlement was calculated as the number of vacancies available (sites unoccupied at the time individuals departed from the communal area) that were closer to the communal area or natal burrow than was their site of final settlement. Only those areas ultimately occupied by a squirrel of the same sex were defined as potential vacancies for moving males and females. Using this criterion males moved on average 3.6 vacancies (range 1-9, $n = 38$) before settling whereas females moved only 1.3 vacancies (range 1-4, $n = 45$). Most females (83%) moved to the vacancy nearest to them - generally an area partially occupied by them already. Males, on the other hand, only moved to the nearest male vacancy in 6 of 16 (38%) of the cases.

The spatial history relative to their natal burrow of yearling females that bred is given in Table 3.10. None of the yearling females that bred dispersed from their natal colony (see also Appendix 15) and all of them lived in the general area of their natal burrows and continued to associate with the same adult neighbours throughout their yearling lives (at least to Period 7). None lived more than 30 m from its natal burrow in Period 7 (Table 3.10). Breeding yearlings lived farthest from their natal burrows during Period 3 (Table 3.10) when 22 of 27 (82%) of them were estimated to have given birth. Period 3 was the time when adult female home ranges were also most separated and showed the lowest amount of overlap with other animals (Fig. 3.2).

In summary, as juveniles, both male and female Columbian ground squirrels at all three colonies resided near their natal burrows and their mothers. Only three (all males) of 130 juveniles lived more than 100 m from their natal sites and close relatives. Most juveniles (89%) lived within 30 m of their natal sites and their mothers. Juveniles emerged the following spring as yearlings away from their natal burrows but near their mothers. Both the mother and her juvenile offspring moved onto common areas away from the natal burrow to hibernate. Once the mother had bred (Periods E or 1) it returned to the area occupied the previous breeding season while its yearling offspring remained on the communal area. Yearlings remained on the communal areas from emergence until Periods 4 or 5. During this

Table 3.10 The mean distance (m) between the activity centres of breeding yearling female Columbian ground squirrels and their natal burrows during the active season.

Period	Mean Distance (m)	Range (m)	Sample Size
E	23.1	4.5-53.7	15
1	22.2	1.4-51.5	24
2	22.7	1.0-49.7	27
3	28.3	4.0-44.4	27
4	23.4	0.0-53.6	27
5	21.4	3.0-45.0	27
6	18.4	1.0-33.8	26
7	17.5	2.0-28.9	23

time male and female yearlings lived an average of 31.6 m and 20.3 m from their natal burrows respectively. Beginning Period 5 and continuing through to Period 6 and early Period 7 many yearling males and females undertook significant shifts in the location of their home range activity centres. Among yearling males 101 of the 139 (73%) were known or presumed to have dispersed from the natal colony. Of the 38 yearling males that remained within the natal colony, 24 (63%) lived more than one adult male HRD from their natal home range or Periods 2-3 centroid (1983 cohort). Among nonbreeding yearling females 40 of 73 (55%) remained in the natal colony; only 13% of them lived more than one adult male HRD away from their natal sites or Periods 2-3 centroid (1983 cohort). The area occupied by yearlings during Periods 7-8 became the areas where these yearlings eventually settled as adults (2- and 3-year olds). After settlement in Periods 7-8 most males, 123 of 139 (88%), lived away (spatially isolated in terms of their 80% core areas) from their natal sites, close kin (mother and littermate sisters), and former adult neighbours, while 48% (35 of 73) of nonbreeding female yearlings settled near their natal sites, close kin and familar adult neighbours. All 29 yearling females that bred remained within one adult male HRD of their natal sites. The only significant shifts in location of activity centres by 2- and 3-year-olds were associated with "migrational" movements to and from the hibernaculum areas each late summer and spring or were associated with the relinquishment of nest sites by adult females to their breeding female offspring.

Discussion

A juvenile Columbian ground squirrel emerges from a maternally defended nest burrow (Festa-Bianchet and Boag 1982, Hackett 1987) and is surrounded by a relatively stable aggregation of neighbours that may include female kin (Festa-Bianchet and Boag 1982, King 1984, Murie and Harris 1984, Wiggett unpubl. data). During the first week above ground juveniles confine their activities to an area around the natal burrow and associate only with their mother and littermate siblings (Waterman 1986, Hackett 1987, pers. obs.). In this study less than 2% of juveniles shifted their activity centres by more than 30 m up to Period 7 - most lived, on average, within 10 m of the natal burrow during this time (Figs. 3.6, 3.7 and 3.8). By Period 8, juveniles had home ranges as large or larger than those of adult females and yearlings (Appendix 7). During Periods 8-10, 11% of juveniles had shifted their home range by 30 m or more. Of these juveniles, 64% were male and three of these males had shifted their home ranges by 175 m or more. Waterman (1986) and Hackett (1987) recorded excursions of juveniles sometimes "hundreds of metres beyond their natal burrows" (Hackett 1987:113) but neither reported any instances of juveniles permanently departing from their natal home ranges. Waterman (1986) reported that male juveniles have a tendency to travel further from the natal burrow than did juvenile females but that male activity centres were no further from their mothers activity centre than were females (supported here in Figs. 3.9 and 3.10).

Sometime before immergence into hibernation juveniles moved onto communal hibernaculum areas where they emerged the following spring. Approximately 26% of all yearlings that emerged each spring were further than one yearling home range diameter (30.0 m for males, 25.0 m for females) away from the natal site as a result of movements onto areas of communal hibernacula. Most adult males and females apparently also overwintered in areas where hibernacula were common (Appendix 10). Mothers and their offspring were associated spatially each spring during emergence even though they all emerged quite a distance from their natal burrows (Figs. 3.9 and 3.10).

Such "migrational" movements of animals onto and off of hibernacula areas each late summer and spring were not reported by Waterman (1986) and Hackett (1987). Both noted, however, that juveniles (and their mother's) hibernated and emerged near the natal burrow and on the maternal home range. Festa-Bianchet and Boag (1982) and Festa-Bianchet and King (1984) observed that during the first two 8-day periods above ground, adult females and yearlings concentrated their activities near the region of a ridge at DC (the colony they studied - see Fig 2.1) which may indicate that the animals emerged from a nearby common area.

The factors that influence differential patterns of hibernation ~~on various~~ study sites are not well known. All three colonies in this study were located on well contoured south-facing slopes of some (up to 20 m) topographic relief. The concentrations of hibernacula on each colony were located in areas where the prevailing winter winds deposited accumulations of snow but with good drainage when the snow melted. Insulating snow cover and adequate spring drainage have been postulated as important factors determining the success of overwintering squirrels (Murie 1985, D.A. Boag pers. comm.). Possibly micro-topographic areas suitable for hibernation were more homogeneously distributed on the areas studied by Waterman and Hackett (where relatively little topographic relief may have prevented differences in snow pack and drainage) than they were at colonies NFE, NFW, RG and possibly DC.

Whatever the cause, differences in the distribution of hibernacula at different colonies resulted in different spatial relations among yearlings and adults. At the colonies studied most animals emerged from one of several hibernacula areas located within each colony. Adult males emerged from hibernation first followed by adult females and yearlings, similar to that reported by Murie and Harris (1982) and Michener (1984). Adults occupied these areas during Periods E and 1 and most breeding took place on these areas. After females had bred, they moved away from the hibernacula areas and established relatively discrete home ranges in areas they had occupied the previous season as adults, or if first-time breeders, in areas on or near the natal area. Yearling males and nonbreeding yearling females remained in the vicinity of the hibernacula areas and formed yearling communal groups. The activities of the yearlings in such groups was concentrated over a relatively small area, interindividual home range overlap was extensive resulting in high densities (eg. as in Figs. 3.3 and 3.4), and these areas were often denuded of vegetative cover by mid season (Table 3.4). Yearling communal groups were composed of sibling subgroups, and were stable in membership and tenure; these groups remained intact from Period E to Periods 4 or 5.

Festa-Bianchet and King (1984:162) reported that "a few places within the meadow [DC - see Chapter 2, Fig. 2.1 and Table 2.1 for description], mainly elevated areas where all vegetation was eliminated by the activity of the squirrels, were consistently used as 'playgrounds'". They observed that such groups were often composed of up to six or seven individuals. Although few details of the spatial association of yearlings and adults were given, those authors did note that most yearlings moved to the central portion of DC, where territorial adult females were absent, at the time when the frequency of adult female aggression had peaked (before and during juvenile emergence). Although Festa-Bianchet and King's yearling "playgrounds" descriptively resemble the yearling "communal" areas described herein, there are a number of important distinctions between the two: at DC yearlings did not live permanently on playground areas, ie. they did not spend the night there nor did they forage exclusively within the bounds of a playground (King, pers. comm.) as yearlings did on my communal areas, and the tenure and number of yearlings on playgrounds changed daily (King, pers. comm.) whereas on communal sites the same yearlings occupied the same space over a lengthy period of time (Periods E to 4 or 5 - Figs. 3.7 and 3.8). One similarity between the two studies is that on both playgrounds and communal areas the activity of yearlings (foraging and play behaviour) reduced vegetative cover relative to surrounding areas (Festa-Bianchet and King 1984).

Hackett (1987) found no evidence for the existence of either playground or communal areas used by yearlings on his four study sites located on an area of continuous meadow. Yearlings in his study emerged in spring on their mothers' home ranges and used burrow systems within 5-10 m of the natal burrow. Mothers and their offspring shared the natal area and maternal home range until Period 3. During Period 3 (parturition) adult females became aggressive and chased all intruders off of their home area including their own yearling offspring. Apparently as a result of this maternal aggression yearlings shifted their activities to the peripheral areas of their mother's home range and established new home areas in the interstices between the mother's home range and those of neighbouring females. Even while living in the interstices between adult female home ranges, yearlings apparently did not live on common areas; in other words, yearlings (with the possible exception of siblings) did not regularly use any area as a playground nor did they reside on communal home areas. Hackett did note overlap, however, between the 80% core areas of yearling siblings while they occupied the interstices between adult female home ranges, but the degree of overlap among such siblings was small relative to the overlap that I observed between yearlings (both siblings and non-siblings) on the communal areas (compare Figs. 3.3 and 3.4 in this study with Figs. 3.11 and 3.12 in Hackett 1987).

Differences in adult-yearling spatial relations may have reflected habitat differences between the sites. At NFW, NFE and RG and possibly DC heterogeneity of topography and aspect may have influenced the distribution of hibernacula such that many hibernacula were concentrated on several small areas within each colony (Appendix 10). On the sites studied by Hackett (1987) micro-topographic variation was less and hibernacula apparently were distributed relatively homogenously since mothers and offspring overwintered on maternal home ranges. In Hackett's study yearlings were able to remain on the maternal home range until parturition (Period 3) when aggression from the mother apparently caused the yearlings to move to the periphery of their maternal home ranges. In my study aggression from reproductively active adult females (mothers or otherwise) apparently inhibited yearlings from leaving the areas from which they emerged (Chapter 4). Had yearlings emerged on the maternal site as they did in Hackett's study, they may have remained on site until parturition when maternal aggression peaked (Chapter 4).

Despite the differences observed in adult-yearling spatial relations, a common pattern emerges from all three studies (Festa-Bianchet and King 1984, Hackett 1987, and this study): maternal aggression results in yearlings living away from adult females whether in the interstices between breeding female home ranges, on playgrounds, or on communal areas (Chapter 4). Apparently yearlings (both males and females) try to isolate themselves spatially from adult females during gestation and lactation (Festa-Bianchet and King 1984, Hackett

1987, Chapter 4). As well, adult males in this study also seemed to avoid adult females after breeding. Males resided generally in areas unoccupied by adult females which often meant that adult males lived with or near yearlings on communal areas. Festa-Bianchet and King (1984) and Hackett (1987) made no mention of the spatial relationships between either adult males and adult females or adult males and yearlings but presumably adult males in their studies were not associated closely with yearlings since no mention was made of the spatial relationship.

In this study, although shifts in home range of $\geq$ 1 home range diameter (HRD) were recorded for all age and sex categories, most squirrels remained relatively sedentary and lived in essentially the same area from period to period and year to year. The only time when shifts in home range were common was among yearlings during Periods 5,6 and 7 (late lactation and juvenile emergence) when most male (73%) and many female yearlings (27%) dispersed or presumably dispersed from their natal colony (Chapter 2, Table 3.1, Fig 3.10). Festa-Bianchet and King (1984) reported that 80% of male and 46% of female yearlings disappeared (presumably dispersed) from colony DC during late lactation and juvenile emergence. Among male yearlings that remained in the natal colony, the majority (61%) shifted their centres of activity such that their 80% core areas no longer overlapped their natal home range, communal area, or the home ranges of their former adult or yearling neighbours. All but two of these males moved more than two adult male HRDs (80 m); one moved 72 m, the other 79 m. On the other hand, few females (7%) that remained within the natal colony permanently settled away from the vicinity of the natal burrow or their mother. Most females that remained in the natal colony lived initially in communal areas away from the natal area, then returned to settle on or near the natal site usually in the company of their mother (Chapter 6). For *S. columbianus*, females generally remain near their birth site and associate with close female kin (mother and sisters) while males usually disperse from their natal home range and relatives (Festa-Bianchet and King 1984, King 1984, Murie and Harris 1984, Hackett 1987). Even in areas of continuous habitat where intercolony movements are relatively uncommon (*cf* Boag and Murie 1981), male yearlings still disperse away from the natal site and female kin. Murie and Harris (1984) reported that 38 of 46 (83%) males lived greater than 100 m from the natal site as adults while Hackett (1987) reported that 73% of male yearlings moved permanently off the natal home range. Thus female philopatry and male dispersal seem to be the norm in all populations of *S. columbianus* studied to date. These patterns of female philopatry and male dispersal are common among ground squirrels (Holekamp 1984) as well as among mammals in general (Greenwood 1980, Dobson 1982). The causes and consequences of these patterns are explored in Chapters 4, 5, and 6.

The definition of dispersal

Researchers often desire to compare nondispersers and dispersers in hopes that such comparisons will help elucidate the causes and adaptive significance of philopatry and dispersal. In species that live in well defined social groups that use a common home range or territory such as primate troops or prairie dog coteries, the distinction between nondispersers and dispersers is easy to make; those individuals that permanently depart from the social group are considered dispersers while those that remain are nondispersers. In solitary territorial species that defend areas containing essential resources, dispersal or lack of it is usually defined in terms of departure from or settlement on the natal (or maternal) home territory.

It is more difficult to define dispersal in species like the Columbian ground squirrel which are territorial (Murie and Harris 1978, Festa-Bianchet and Boag 1982, Hackett 1987), but which also form relatively stable social aggregations of kin and neighbouring conspecifics. In a case such as this, is dispersal best defined in terms of the natal site or in terms of the social "group"? The answer depends of course, on the question asked. If one is interested in comparing philopatry and dispersal relative to the costs and benefits associated solely with the natal site then dispersal is probably best defined in terms of settlement on or departure from the natal site. If questions of kinship and/or familiarity are important then dispersal is best defined in relation to the social group rather than to any particular physical area.

In this study movements of animals to the area of final settlement could be classed into two categories: 1) those individuals that remained on or near the natal home range and retained proximity to former spatial associates, and 2) those individuals that departed permanently from their natal site and their former neighbours.

No instances were recorded where individuals moved away from spatial associates yet still occupied a portion of the natal home range or vice versa. Since there are probably advantages and disadvantages related to moving away from both the natal site and spatial associates (Sherman 1976, Waser and Jones 1983, Murie and Harris 1984, Hackett 1987) dispersal is probably best defined (at least in this study) as the permanent departure of individuals from their place of birth *and* from their former neighbours.

Interestingly, all but two individuals, that eventually settled away from the natal site and their former spatial associates, moved by two or more adult male HRDs ($\geq$ 80 m). The two exceptions were males that moved 71 m and 79 m from their natal burrows. Prior to settlement these two males had neighbours on only one side of their home ranges. After settlement these males isolated themselves from their former neighbours in a more peripheral location and no longer were seen to interact or come in contact with any former neighbours and thus effectively moved more than two HRDs. In this study all home range shifts of two or more HRDs ($\geq$ 80 m) could be considered as dispersal movements.

Nondispersers were those individuals that permanently settled on or near the natal site and that retained essentially the same adult neighbours both before and after final "settlement" (Periods 7-8 yearling centroid). Dispersers on the other hand left the vicinity of both their natal site and their former spatial associates. Dispersers could be categorized as intercolony dispersers (Chapter 2) and intracolony dispersers (those animals that dispersed by the above definition but that remained in their natal colony).

In all studies, no matter how dispersal is defined the classification of individuals into dispersers and nondispersers will always be somewhat arbitrary. As long as the definition used is appropriate for the question asked and is clearly defined for the reader the definition will be legitimate and useful.

General conclusions

An important generality emerges from this study; the spatial relations and organization of individuals within a population is not predetermined and invariant. Apparently environmental constraints such as resource limitation (Dobson and Murie 1987) or habitat structure (Webb 1981, this study) influences how animals space themselves and interact. In light of these findings it becomes increasingly apparent that the social organization, demography and behaviour of species cannot be generalized until a number of populations has been studied (*cf* Slade and Balph 1974 for similar arguments). In cases where populations differ in social structure, one can expect the proximal causes of certain socially induced behaviours (eg. dispersal) to differ. In the next Chapter I examine whether the hypothesized cue to dispersal, conspecific aggression (Festa-Bianchet and King 1984, Hackett 1987), is sufficient to cause dispersal of yearlings from my study sites where the spatial relations differed from that reported by these other authors.

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IV. Social Behavioural Correlates of Natal Dispersal in the Columbian Ground Squirrel

Introduction

Dispersal in some species seems to be socially induced, while in others, it apparently occurs independent of social interactions (for reviews see Gaines and McClenaghan 1980, Greenwood 1980, Greenwood and Harvey 1982, Holekamp 1984, Pusey and Packer, 1987). Among ground squirrels that disperse as juveniles, Holekamp (1984) concluded that natal emigration by juvenile males was independent of social interactions, but for juvenile females such movements were related to aggression received on the natal home range from the mother and/or sisters. Among species of ground squirrels which delay dispersal until age 1 or 2 years, emigration appears to be dependent upon conspecific aggression (Armitage and Downhower 1974, Downhower and Armitage 1981, Festa-Bianchet and King 1984, Brody and Armitage 1985, Hackett 1987).

For populations of Columbian ground squirrels (*Spermophilus columbianus*) in southwestern Alberta, where dispersal is delayed until the animals are 1-year-olds, conspecific aggression has been postulated to cause natal emigration by both males and females (Festa-Bianchet and King 1984, Hackett 1987). Festa-Bianchet and King (1984) reported evidence which suggested that dispersal of yearling *S. columbianus* was initiated by aggressive interaction with adults of both sexes and with yearling conspecifics. Hackett (1987) determined that aggression from reproductively active mothers and intersibling competition were the proximal stimuli causing dispersal in populations of this species that he studied.

I studied *S. columbianus* in areas where the spatial relations among adults and yearlings differed from those reported by Festa-Bianchet and King (1984) and Hackett (1987)(Chapter 3). Instead of residing on the natal home range with the mother and littermate siblings, yearlings on my study sites usually lived away from the natal area and occupied areas in common with other yearlings (sibs and nonsibs) and with adult males (Chapter 3). Given these differences in spatial relations, I predicted that if conspecific aggression initiated emigration, the individual animals providing the stimuli should differ between populations with different spatial and social structures.

The purpose of this study was to determine whether conspecific aggression initiated dispersal of yearling Columbian ground squirrels in three isolated populations in southwestern Alberta, and, if so, whether the conspecifics differed where the spatial relations among conspecifics also differed.

Methods

The behaviour of individual Columbian ground squirrels was studied at colonies NFW, NFE, and RG from 1984-1986. Details of location and size of each colony are given Figs 2.1, and 2.6, and Table 2.1 in Chapter 2. Demographic parameters for each colony studied are given in Appendices 8 and 9.

All squirrels at each colony were individually identifiable by serially numbered eartags (one in each ear) and unique body dye marks (see Chapter 2 for further details). Age (or minimum age) and sex of each animal was known as were the matrilineal relationships of all animals born in these colonies in 1984 and 1985 (see Chapters 2 and 5 for further details). Weight and reproductive status of animals were determined at regular intervals as outlined in Chapters 2 and 3.

Squirrels were observed from 2-3 m tall observation towers (one in each colony) with the aid of 10 X 50 binoculers or 20 - 45 X 60 spotting scopes. Locations of sighted animals were estimated to the nearest meter on both the x and y coordinates of a grid system established at each colony at the outset of the study (Chapter 3). The estimated coordinates recorded from the observation towers were accurate to within less than 1 m at each colony (NFW = 0.95 m, NFE = 0.8 m, RG = 0.6 m) when compared with actual measured distances on the ground.

Each morning, observations were initiated when the first squirrel emerged (usually between 0600 and 0700 hrs MST) and were continued until 3 hours had elapsed (Chapter 3).

Squirrels that resided in peripheral areas of NFW and NFE, not readily visible from observation towers, were observed during short 15-30 minute "peripheral" scans that followed the 3-hour observation period (Chapter 3).

For purposes of analysis, the active season at each colony was divided into 11 10-day intervals as outlined in Chapter 3. Each colony was aligned to a common event in the reproductive cycle. Day 60 (the 1st day of period 6), the median date of juvenile emergence, was used at each site. The majority (>85%) of females bred during Days 1-13 and gave birth during Days 25-37. Most juveniles (>85%) emerged for the first time during Days 53-65. In 1984 observations began during Period 1 at NFE, Period 2 at NFW, and Period 3 at RG and continued until immergence began in Period 10. During 1985 and 1986 observations were initiated as soon as squirrels were emerging from hibernation (Period E, Days 1-9, in all cases) and were continued in 1985 until immergence began (Period 10, Days 100-109) and in 1986 until the end of dispersal (Period 7, Days 70-79, Chapter 3).

Observations were made using scan sampling (Altmann 1974, Lehner 1979) for adults and juveniles and "focal-scan" sampling for yearlings (for details see Appendix 4). At each colony scans were conducted from left to right across the colony. For each sighting of an adult or juvenile, the time and the individual's identity, location, and behaviour were recorded. At each sighting of a yearling the identity, location, behaviour, and time of sighting were recorded as were the identity, location, and behavior of all conspecifics that were within 10 m of the yearling in question. The yearling and all conspecifics that occurred within 10 m of the yearling were observed for 2 minutes. Any interactions between the "focal" yearling and its nearby conspecifics were recorded. Only when animals co-occurred with each other in time (during 2-min periods) and space (within 10 m) were they considered to be "available" to interact (Appendix 4). Interaction rates between pairs of animals was calculated as the number of interactions divided by the number of times the pair co-occurred in time and space (the number of "spatio-temporal" overlaps). Interaction frequency for a pair of animals was calculated as the number of interactions divided by the number of "scans" (15-min intervals) within which the two animals were simultaneously sighted. Interaction frequency was simply a measure of the frequency of interaction over time whereas interaction rate was a measure of the rate of interaction between individuals when given the "opportunity" (spatio-temporal overlap) to interact (Appendix 4). There was no time component to interaction rates since the duration of spatio-temporal overlap between individuals was not measured.

Interaction rates between two age/sex categories were the interaction rate of one group towards the other and not the *mutual* rate of interaction. For example, the agonistic interaction rate between adult and yearling males was calculated differently from that between yearling and adult males. In the former case, the agonistic rate was calculated as the number of times that adult males interacted aggressively towards yearling males divided by the number of spatio-temporal overlaps (STO's) between adult and yearling males. In the latter case, it was calculated as the number of times yearling males interacted aggressively towards adult males divided by the number of STO's. Calculated in this way the contribution of each cohort to the interaction rate of the two groups as a whole is known; this is particularily important where interactions between cohorts are asymmetric.

A description of the social and nonsocial behaviours sampled are given in Appendix 16. Social interactions were classed into four categories; aggressive, cohesive, recognitive, and ambiguous. Aggressive behaviours always resulted in the displacement of one or both animals of an interacting pair whereas cohesive behaviours always involved close physical contact without displacement (see Appendix 16 for further details). Behaviours such as charges, chases, lunges, and fights were considered agonistic whereas allogrooming, bodily contact, and physical close proximity were considered cohesive. Recognitive behaviours consisted of the "greeting" behaviours described by Steiner (1970) and Betts (1976). Ambiguous behaviours were social behaviours that could not be readily classified as agonistic, cohesive, or recognitive; and hence were ambiguous in context. When two animals interacted, the entire sequence of behaviours comprising that interaction was classed into one of the four behavioural categories. For instance, animal A approaches animal B (ambiguous), they "greet" (recognitive) and then A lunges at B (agonistic) and chases B for 10 m (agonistic). Even though the interaction contained ambiguous, recognitive, and agonistic components, the components were considered secondary in importance to the *outcome* of the entire interaction. Since one animal forcibly displaced another, the entire interaction was considered agonistic. Thus in calculating rates of social interaction the number of social encounters and their outcome was used; not the number of behaviours involved.

For purposes of analysis, only agonistic and cohesive interactions, which comprised the majority of the interactions (81% - see Appendix 17), were used. Since the general context of ambiguous interactions was unknown it seemed most appropriate to eliminate them from the analysis. Recognitive behaviours were normally a component of both agonistic and cohesive interactions and as such rarely stood alone as a complete interaction. Thus, it seemed appropriate to eliminate recognitive interactions from the analysis as well.

Data from all three colonies (NFW, NFE, and RG) and 2 years (1985 and 1986) were combined for the purpose of analysis. Data from 1984 were not included because in that year the "focal-scan" sampling regime was not used to sample behavioural interactions. Such a regime was necessary to determine interaction rates accurately (see Appendix 4). Although there was great individual variation in interaction rate, the general patterns of interaction within colonies between years and between colonies within years were similar (Appendix 18a, b). Most of the differences in interaction rates between colonies and years probably resulted from small sample sizes. Combining colonies and years facilitated presentation and increased sample sizes and individual variability became less of a confounding factor where samples were large (Sokal and Rohlf 1981).

Rates and frequencies of agonistic and cohesive behaviour among yearlings and between yearlings and adults were compared for males and females, as well as for nondispersers, and intracolony and intercolony dispersers. Nondispersers were individuals that as adults settled on or near their natal home range and near familiar neighbouring conspecifics (see Chapter 3 for further discussion). Dispersers permanently departed from both the area where they were born and their former neighbours. Intracolony dispersers settled away from their natal site and former neighbours but remained within the confines of the natal colony whereas intercolony dispersers permanently departed from the natal colony. Intercolony dispersers were composed of presumed dispersers, those that disappeared from the natal colony during the dispersal period (Chapters 2 and 3) and were never seen again, and known dispersers, those that were captured subsequently in a non-natal colony elsewhere. Collectively, "dispersers" refer to intracolony plus intercolony dispersers.

Within sex, dominance relationships among yearlings were analysed using dominance matrices (Lehner 1979). Dominance status of individual yearlings relative to that of other members of the yearling cohort living in the same "communal" area (Chapter 3) was compared for nondispersers, and intracolony and intercolony dispersers. Play behaviour (Steiner 1970, Betts 1976, Festa-Bianchet and King 1984) was not used to determine dominance relationships. Instead only aggressive encounters between yearlings were used to assess dominance. During an interaction one squirrel was considered to dominate another if that squirrel succeeded in displacing the other from the vicinity of the interaction.

Statistical procedures follow those outlined in Sokal and Rolph (1981) and Zar (1981). Nonparametric statistical inference was applied since the data did not meet assumptions necessary for parametric statistics. Even so, the probability of a Type 1 error occurring has been postulated to be artificially high when ethological data are compared using nonparametic statistics because of the problem of interdependency of data (Machlis *et al.* 1986). Thus the tests presented herein should be viewed cautiously especially when significance levels are near 0.05.

Results

Adult-yearling interactions

General rates and frequencies of agonistic and cohesive interactions of adult males and females towards yearling males and females over time are given in Figs. 4.1 and 4.2. Aggressiveness of adult males towards yearling males and females was high for most of the active season except during Periods E, 1, and 9 (Fig. 4.1a). Aggressiveness peaked during Periods 5 and 7 for females and Period 7 for males (Fig. 4.1a). There were no significant differences in the rate at which adult males interacted aggressively towards yearling males or females except during Period 5 when adult males were more aggressive towards females than they were to males (Fig. 4.1a). The frequency (number of interactions per scan) during which adult males interacted aggressively towards yearlings, did not differ between male and female yearlings (Fig. 4.1b). For both sexes the frequency of aggression peaked during Period 3 and was variable but generally declined thereafter (Fig. 4.1b). Adult male-yearling cohesive rates were highest early in the active season (during Periods E-4) gradually declining to zero just before immergence in Period 10 (Fig. 4.1c). Generally adult males interacted more cohesively towards yearling females than towards yearling males but these differences were significant only during Periods 3 and 4 (Fig 4.1c).

Two-year-old males were significantly more aggressive towards yearling males but not yearling females, than were older (3-year-old and older) adult males (Table 4.1). No differences were recorded in rates of cohesive behaviour between 2-year-old and older adult males with either yearling males or females (Table 4.1). Those yearling males that shared the communal area (see Chapter 3) with 2-year-old males dispersed from the communal area at a slightly greater rate (88%, n = 25) than did those yearling males that shared communal areas with older (3-year or older) adult males (73% , n = 60); these differences, however, were not significant ($X^2 = 2.187$; $0.25 \geq P \geq 0.10$).

Adult female aggressiveness towards yearling males and females peaked during Periods 2 and 3 (parturition) and Periods 5 and 6 (juvenile emergence) (Fig. 4.2a). After Period 7 the aggressiveness of adult females towards yearlings decreased rapidly (Fig. 4.2a). Yearling

Fig. 4.1. Agonistic interaction rate (a), frequency (b), and cohesive interaction rate (c) of adult males towards yearling male and female Columbian ground squirrels over time. All colonies (NFW, NFE, and RG) and years (1985 and 1986) combined. Females that bred as yearlings are excluded. Sample sizes for each sex are given above each time period. •————• yearling males, •– – – – – –• yearling females. * = $P \leq 0.05$, ** = $P \leq 0.01$

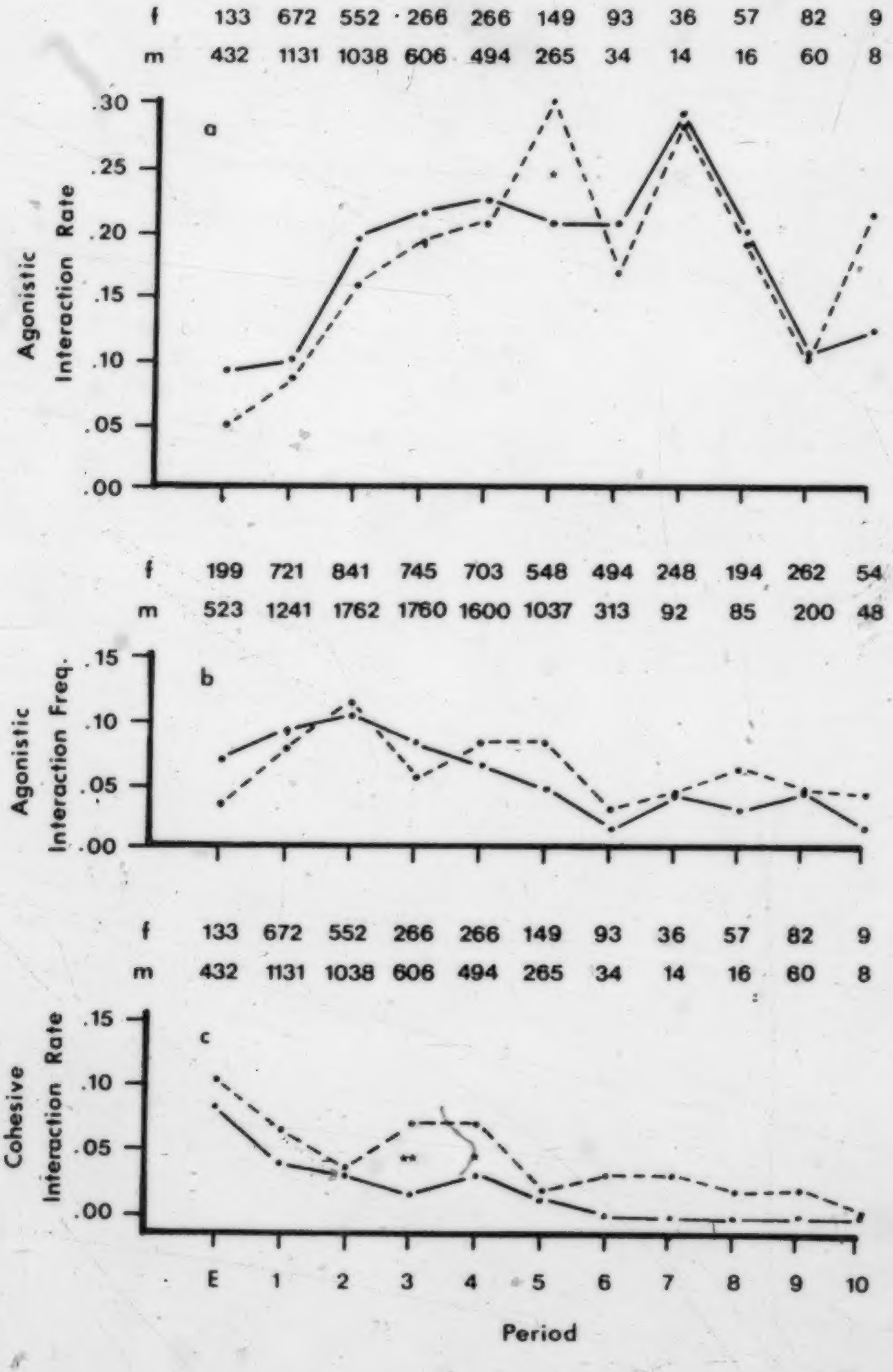
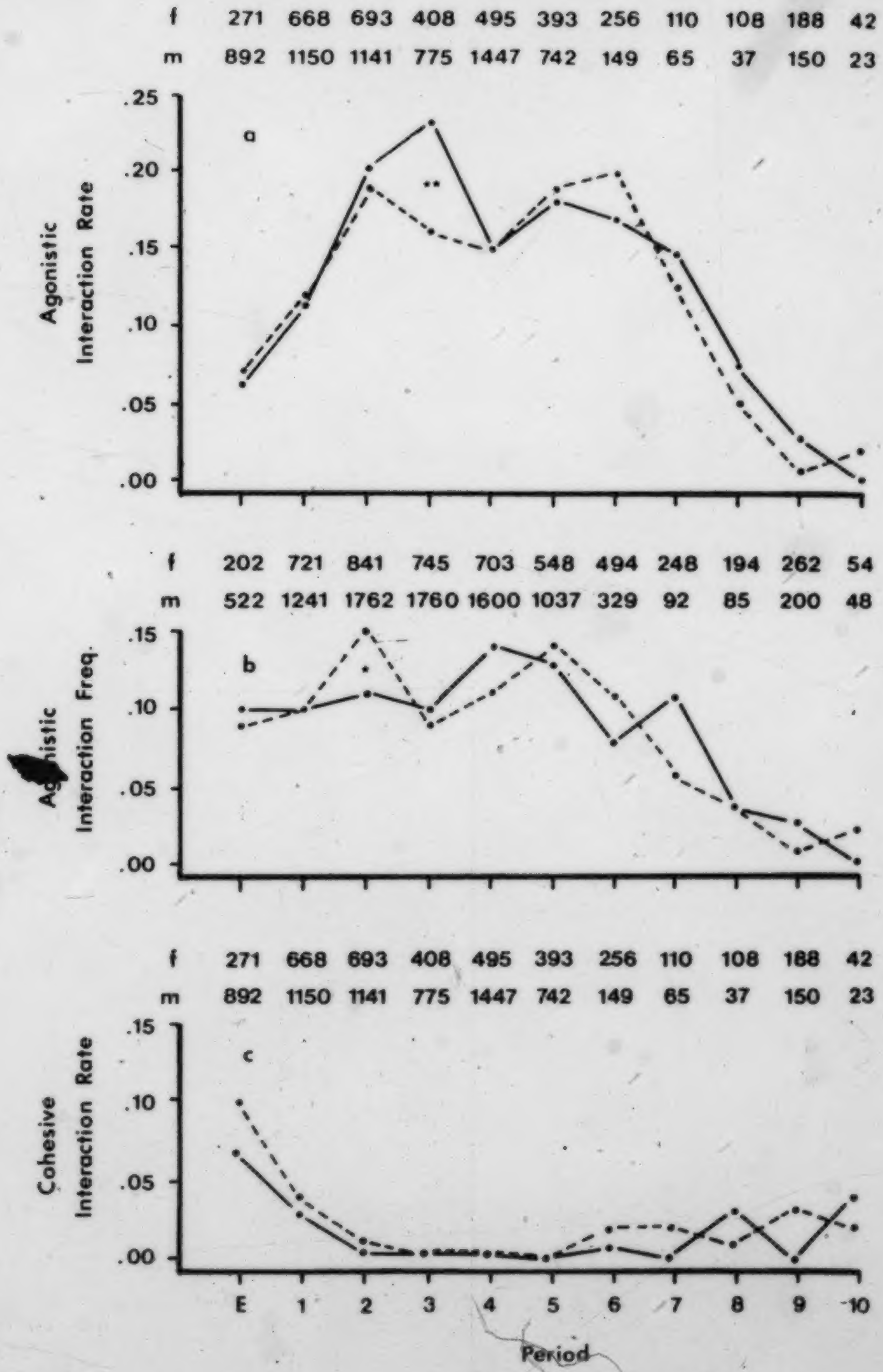

f 133 672 552 266 266 149 93 36 57 82 9
m 432 1131 1038 606 494 265 34 14 16 60 8
Agonistic Interaction Rate
.30
.25
.20
.15
.10
.05
.00
a
f 199 721 841 745 703 548 494 248 194 262 54
m 523 1241 1762 1760 1600 1037 313 92 85 200 48
Agonistic Interaction Freq.
.15
.10
.05
.00
b
f 133 672 552 266 266 149 93 36 57 82 9
m 432 1131 1038 606 494 265 34 14 16 60 8
Cohesive Interaction Rate
.15
.10
.05
.00
c
**
E 1 2 3 4 5 6 7 8 9 10
Period

Table 4.1 Agonistic and cohesive interaction rates between 2-year-old and older adult males with yearling males and females. Data are combined from colonies NFW, NFE, and RG and years 1985 and 1986. Excluded were females that bred as yearlings. Number of spatio temporal overlaps are given in parentheses.

	Agonistic Interaction Rate		Difference[1]	Cohesive Interaction Rate		Difference[1]
	with 2-year-old males	with older males		with 2-year-old males	with older males	
Yearling males	0.19 (1803)	0.14 (1485)	$\underline{P} \leq 0.01$	0.03 (1803)	0.03 (1485)	$\underline{P} > 0.05$
Yearling females	0.16 (319)	0.16 (358)	$\underline{P} > 0.05$	0.07 (319)	0.06 (358)	$\underline{P} > 0.05$

[1] Chi^2 test

Fig. 4.2. Agonistic interaction rate (a), frequency (b), and cohesive interaction rate (c) of adult females towards yearling male and fema Columbian ground squirrels over time. All colonies (NFW, NFE, and RG) and years (1985 and 1986) combined. Females that bred as yearlings are excluded. Sample sizes for each sex are given above each time period. •———————• yearling males, •- - - - - -• yearling females. * = $P \leq 0.05$, ** = $P \leq 0.01$ (X^2 test).


f 271 668 693 408 495 393 256 110 108 188 42
m 892 1150 1141 775 1447 742 149 65 37 150 23
a
**
Agonistic Interaction Rate
.25
.20
.15
.10
.05
.00
f 202 721 841 745 703 548 494 248 194 262 54
m 522 1241 1762 1760 1600 1037 329 92 85 200 48
b
*
Ag[illegible]istic Interaction Freq.
.15
.10
.05
.00
f 271 668 693 408 495 393 256 110 108 188 42
m 892 1150 1141 775 1447 742 149 65 37 150 23
c
Cohesive Interaction Rate
.15
.10
.05
.00
E
1
2
3
4
5
6
7
8
9
10
Period

males and females were not treated differently except during Period 3 when adult females interacted aggressively towards yearling males more often than against yearling females (Fig. 4.2a). The frequency of adult female aggressiveness towards yearlings was relatively constant until Period 6 (Fig. 4.2b). On average adult females interacted aggressively towards male and female yearlings in 11% of the scans in which yearlings were sighted during Periods E to 6. The frequency of agonistic behaviour declined to near zero over Periods 7 to 10 (Fig. 4.2b).

The rate of cohesive interactions between adult females and yearlings was highest early in the season (Periods E and 1) and late in the season (periods 8, 9 and 10) (Fig. 4.2c). Adult females did not interact cohesively with yearlings from Period 2 (late gestation/parturition) to Period 5 (juvenile emergence) (Fig. 4.2c). Male and female yearlings were not treated differently by adult females with regard to cohesive social behaviours (Fig. 4.2c).

There were few differences in either interaction rates or frequency of aggression by adult males towards yearling male nondispersers, intracolony or intercolony dispersers (Fig. 4.3). Only during Period 3 did adult males interact aggressively towards intracolony dispersers at a higher rate and frequency than towards nondispersing and intercolony dispersing yearling males. On the other hand, adult males apparently treated yearling female dispersers and nondispersers differently. Yearling females that ultimately dispersed (or presumably dispersed) were involved in more aggressive interactions and at higher rates than were yearling female nondispersers, the differences being significant during two periods (Fig. 4.3). Although differences were noted in aggressiveness, none was observed in cohesiveness; adult males interacted cohesively equally with nondispersers and dispersers and with males and females (Table 4.2).

Rates of aggressiveness by adult females toward yearling male nondispersers, intracolony and intercolony dispersers differed signficantly during Periods 2, 3 and 4 (Fig. 4.4). During these periods and subsequently during Periods 5 and 6 dispersers were involved more often in aggressive interactions than were nondispersers (Fig. 4.4). Similarily, dispersers

Fig. 4.3. Agonistic interaction rate and frequency of adult males towards yearling Columbian ground squirrels; comparison of dispersers and nondispersers. All colonies (NFW, NFE, and RG) and years (1985 and 1986) combined. Females that bred as yearlings are excluded. Sample sizes for each dispersal category are given above each time period. For yearling males: •————• nondispersers(ND), •·········• intracolony dispersers(IAD), •– – – – – –• intercolony dispersers(IED). For yearling females; •————• nondispersers(ND), •– – – – – – –• dispersers(D). * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$ (X^2 Test).

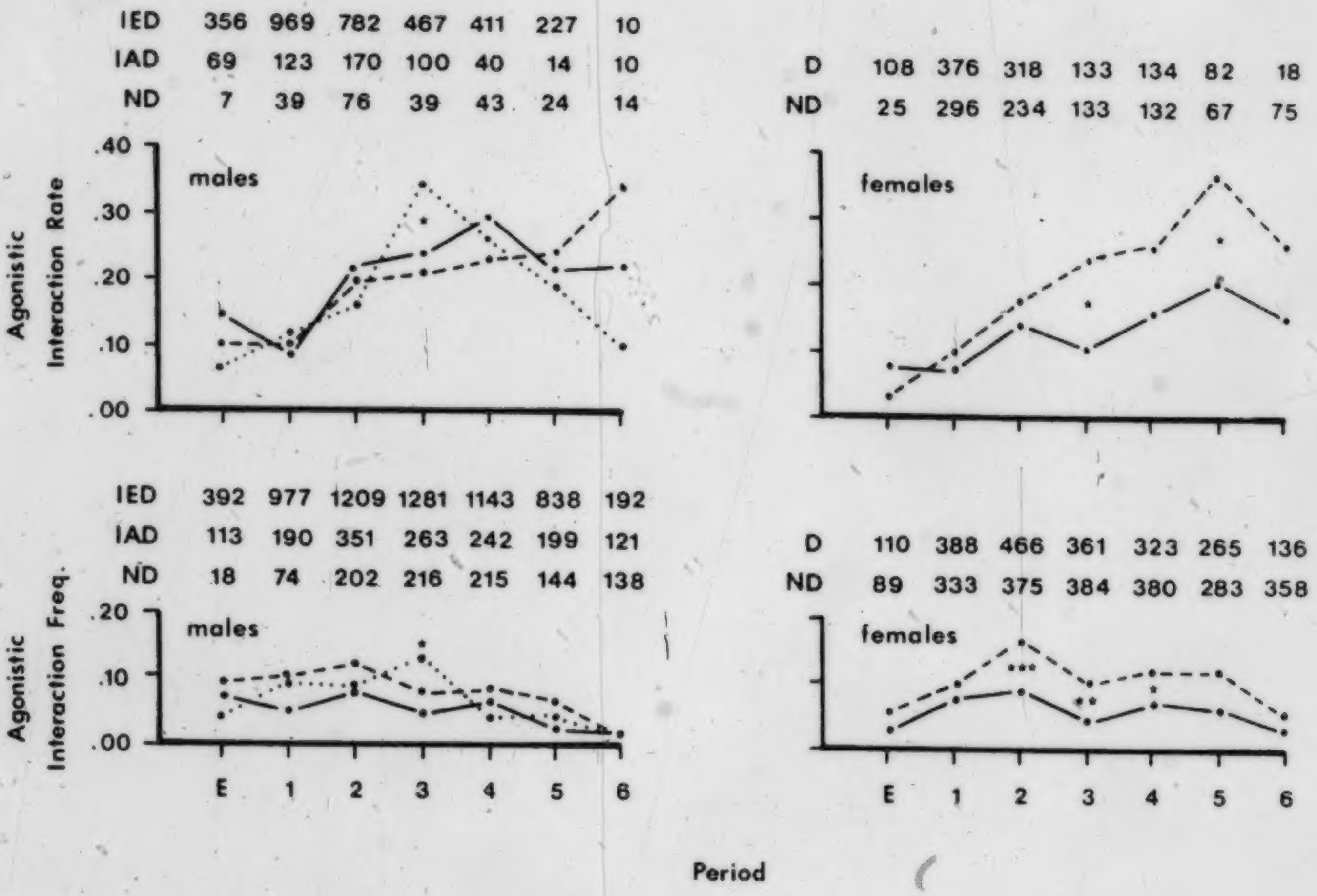
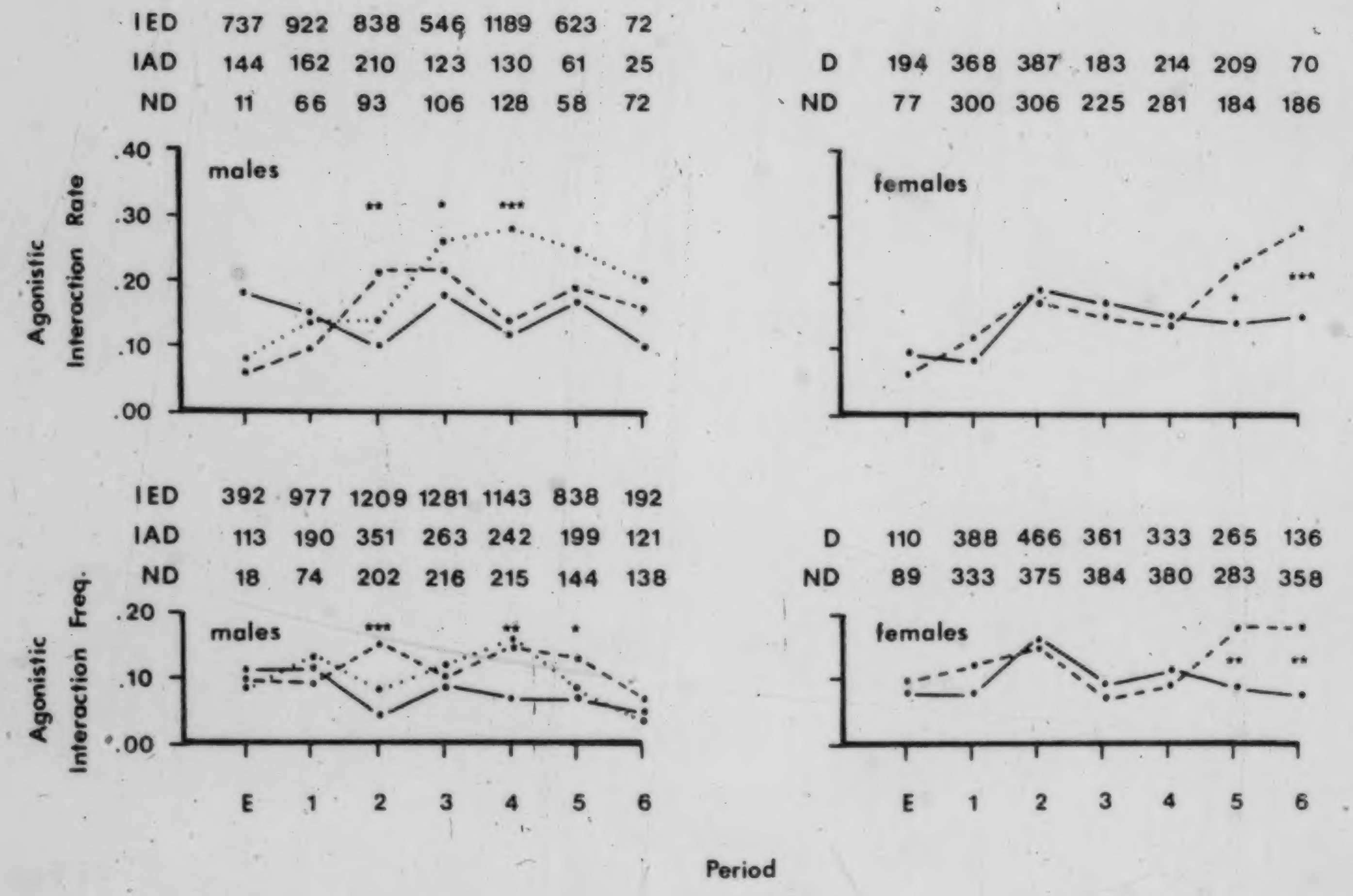

IED 356 969 782 467 411 227 10
IAD 69 123 170 100 40 14 10
ND 7 39 76 39 43 24 14
D 108 376 318 133 134 82 18
ND 25 296 234 133 132 67 75
Agonistic Interaction Rate
.40
.30
.20
.10
.00
males
females
IED 392 977 1209 1281 1143 838 192
IAD 113 190 351 263 242 199 121
ND 18 74 202 216 215 144 138
D 110 388 466 361 323 265 136
ND 89 333 375 384 380 283 358
Agonistic Interaction Freq.
.20
.10
.00
males
females
E 1 2 3 4 5 6
E 1 2 3 4 5 6
Period

Table 4.2 Cohesive interaction rate among Columbian ground squirrels to Period 6 for yearling males and females with adult males and females. All colonies (NFW, NFE, and RG) and years (1985, 1986) combined. Excludes females that bred as yearlings. Number of spatial-temporal overlaps given in parentheses.

	Adult Male			Adult Female		
	Yearling male	Yearling female	Difference[1]	Yearling male	Yearling female	Difference[1]
Nondispersers	0.03 (363)	0.06 (959)	$\underline{P} > 0.05$	0.01 (641)	0.02 (2149)	$\underline{P} > 0.05$
Intracolony dispersers	0.03 (409)	-	-	0.02 (741)	-	-
Intercolony dispersers	0.04 (3215)	0.05 (1143)	$\underline{P} > 0.05$	0.02 (4385)	0.03 (1617)	$\underline{P} > 0.05$
Difference	$\underline{P} > 0.05$	$\underline{P} > 0.05$	-	$\underline{P} > 0.05$	$\underline{P} > 0.05$	-

[1] Chi^2 test

Fig. 4.4. Agonistic interaction rate and frequency of adult females towards yearling Columbian ground squirrels; comparison of dispersers and nondispersers. All colonies (NFW, NFE, and RG) and years (1985 and 1986) combined. Females that bred as yearlings are excluded. Sample sizes for each dispersal category are given above each time period. For yearling males; •————• nondispersers(ND), •··········• intracolony dispersers(IAD), •-------• intercolony dispersers(IED). For yearling females, •————• nondispersers(ND), •------• dispersers(D). * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$ (X^2 test).


IED 737 922 838 546 1189 623 72
IAD 144 162 210 123 130 61 25
ND 11 66 93 106 128 58 72
males
** * ***
Agonistic Interaction Rate
.40
.30
.20
.10
.00
D 194 368 387 183 214 209 70
ND 77 300 306 225 281 184 186
females
* ***
IED 392 977 1209 1281 1143 838 192
IAD 113 190 351 263 242 199 121
ND 18 74 202 216 215 144 138
males
*** ** *
Agonistic Interaction Freq.
.20
.10
.00
D 110 388 466 361 333 265 136
ND 89 333 375 384 380 283 358
females
** **
E 1 2 3 4 5 6
E 1 2 3 4 5 6
Period

were involved in aggressive interactions more frequently with adult females than were nondispersers; significantly so during Periods 2, 4 and 5 (Fig. 4.4). The rate and frequency of aggression between adult females and yearling female nondispersers and dispersers did not differ significantly until Periods 5 and 6 (juvenile emergence) when dispersers were involved in more aggressive interactions and at greater rates than were nondispersers (Fig. 4.4). Adult females interacted equally cohesively with male and female yearlings as well as with nondispersing and dispersing yearlings (Table 4.2).

The number of spatio-temporal overlaps per scan observed for yearling males and females with adult males and females are given in Figs. 4.5 and 4.6. The number of spatio-temporal overlaps per scan provides an index of the frequency of spatio-temporal coincidence of cohorts over time. The frequency of overlap between adult and yearling males, and adult males and yearling females did not differ significantly except during Period E (Fig. 4.5a). The frequency of adult male-yearling spatial overlap decreased steadily from a peak of 0.96 in Period 1 to a low of 0.20 in Periods 6 and 7; thereafter the degree of spatio-temporal overlap was variable but remained low (Fig. 4.5a). Male nondispersers, intracolony and intercolony dispersers differed significantly in the frequency of spatio-temporal overlap with adult males. Generally nondispersers had the least frequent overlap with adult males, followed by intracolony dispersers and intercolony dispersers which had the greatest frequency of overlap with adult males (Fig. 4.5b). Female dispersers and nondispersers differed in the frequency of overlap with adult males only during Periods E, 1 and 2; thereafter no differences were recorded (Fig. 4.5c). When there were differences, dispersers had more frequent contact with adult males than did nondispersers.

Although the general patterns of frequency of spatio-temporal overlap with adult females were similar for yearling males and females, there were significant differences between the two sexes in 6 of the 11 periods (Fig 4.6a). In three periods (E, 4 and 7) males had a significantly greater overlap with adult females than did yearling females. In Periods 2, 3 and 10 females had a significantly greater frequency of overlap with adult females than did

Fig. 4.5. Number of spatio-temporal overlaps (STO's) per scan for yearling males and females with adult male Columbian ground squirrels; comparison of males and females and nondispersers and dispersers. All colonies (NFW, NFE, and RG) and years (1985 and 1986) combined. Females that bred as yearlings are excluded. Sample sizes are given above each time period. For yearlings: •————————• male(M), •– – – – – – –• female(F). For males, •————————• nondispersers(ND), •...........• intracolony dispersers(IAD), •– – – – – – –• intercolony dispersers(IED). For females; •————————• nondispersers(ND), •– – – – – – –• dispersers(D). * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$ (X^2 test).

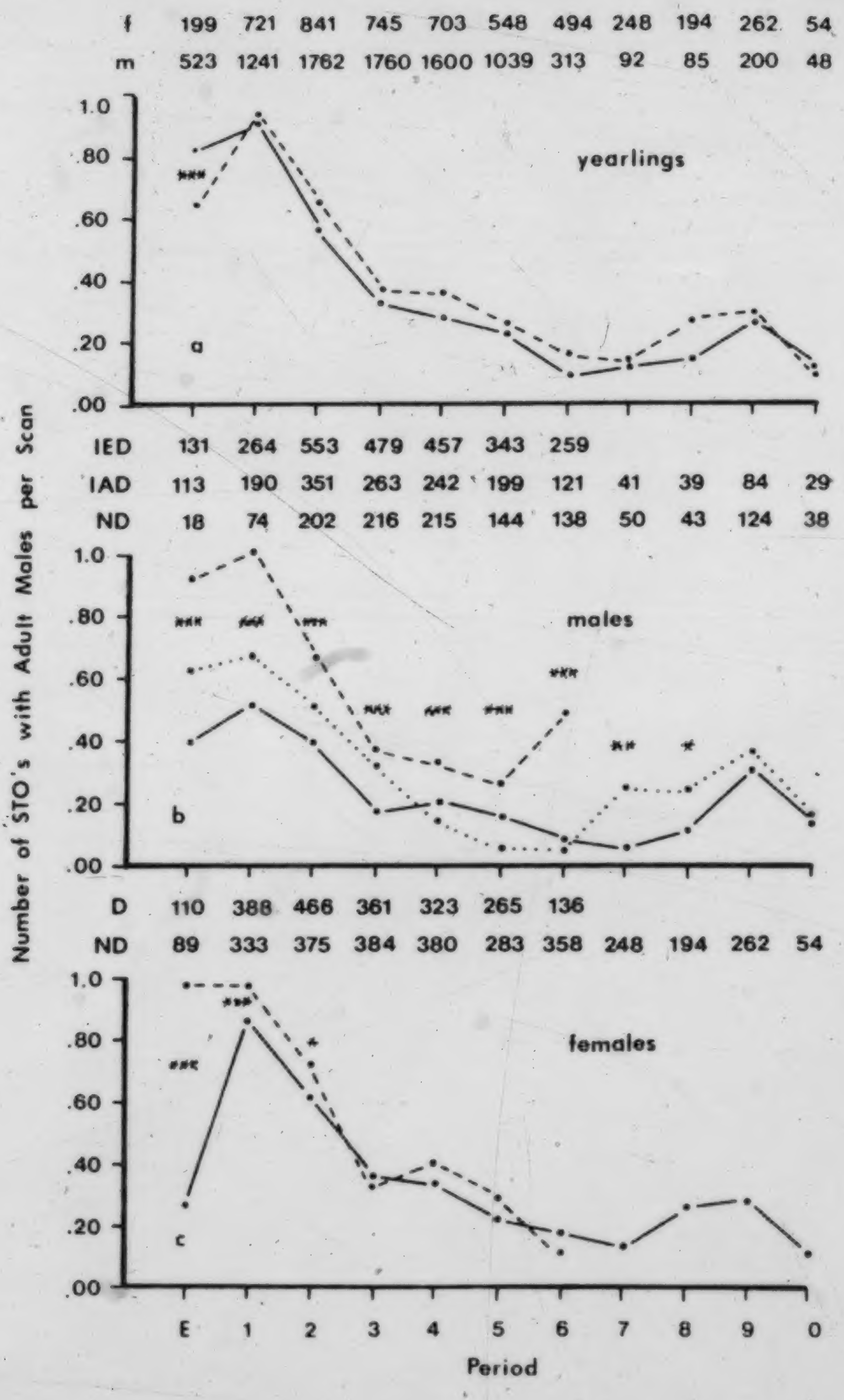
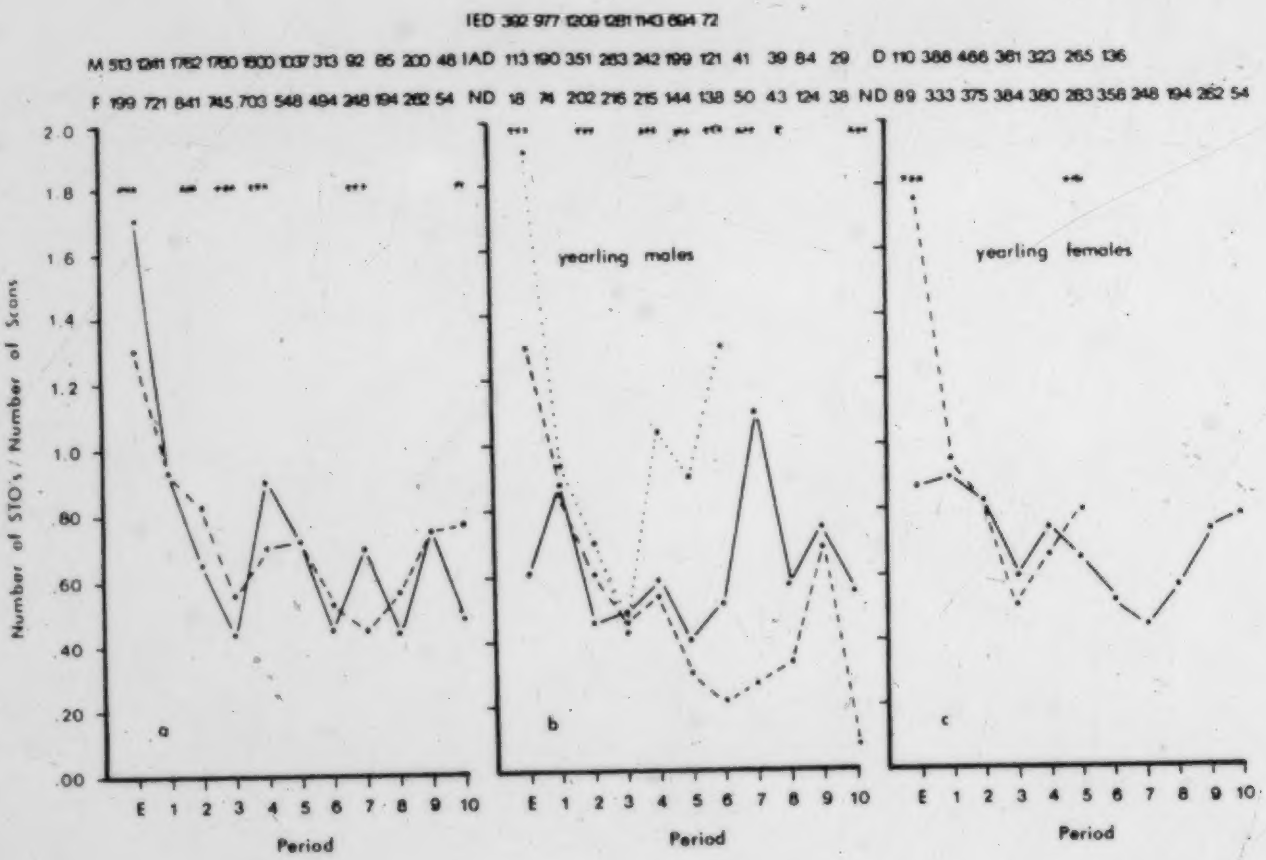

f 199 721 841 745 703 548 494 248 194 262 54
m 523 1241 1762 1760 1600 1039 313 92 85 200 48
1.0
.80
.60
.40
.20
.00
yearlings
***
a
IED 131 264 553 479 457 343 259
IAD 113 190 351 263 242 199 121 41 39 84 29
ND 18 74 202 216 215 144 138 50 43 124 38
males
*** *** *** *** *** *** *** ** *
b
D 110 388 466 361 323 265 136
ND 89 333 375 384 380 283 358 248 194 262 54
females
*** *** *
c
Number of STO's with Adult Males per Scan
E 1 2 3 4 5 6 7 8 9 0
Period

Fig. 4.6. Number of spatio-temporal overlaps (STOs) per scan for yearling males and females with adult female Columbian ground squirrels; comparison of males and females and nondispersers and dispersers. All colonies (NFW, NFE, and RG) and years (1985 and 1986) combined. Females that bred as yearlings are excluded. Sample sizes are given above each time period. For yearlings: •————• male(M), •- - - - - - -• female(F). For males, •————• nondispersers(ND), •··········• intracolony dispersers(IAD), •- - - - - - -• intercolony dispersers(IED). For females; •————• nondispersers(ND), •- - - - - - -• dispersers(D). * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$ (X^2 test).


IED 392 977 1209 1281 1143 694 72
M 513 1241 1762 1780 1800 1037 313 92 86 200 48
F 199 721 841 745 703 548 494 248 194 282 54
IAD 113 190 351 283 242 199 121 41 39 84 29
ND 18 74 202 216 215 144 138 50 43 124 38
D 110 388 466 361 323 265 136
ND 89 333 375 384 380 283 356 248 194 262 54
Number of STO's / Number of Scans
2.0
1.8
1.6
1.4
1.2
1.0
.80
.60
.40
.20
.00
a
b
c
yearling males
yearling females
E
1
2
3
4
5
6
7
8
9
10
Period

males.

Except for Periods 1, 3, and 9, yearling male nondispersers, intra- and intercolony dispersers differed significantly in the frequency of spatio-temporal overlap with adult females (Fig. 4.6b). During Periods E to 6 nondispersers averaged 0.53 STO's/scan whereas intracolony dispersers averaged 0.58 and intercolony dispersers 0.86 STO's/scan. These differences are statistically different (X^2 = 698.7, $P \leq 0.001$) as are the differences between male nondispersers and both classes of dispersers combined (0.56 versus 0.82 respectively, X^2 = 865.1, $P \leq 0.001$).

A similar trend was noted for yearling female nondispersers and dispersers. Generally dispersing females had a greater frequency of overlap with adult females than did yearling nondispersers (Fig. 4.6c). During periods E to 6 nondispersing yearling females averaged 0.71 STO's/ scan with adult females compared to 0.84 for yearling female dispersers (X^2 = 40.86, $P \leq 0.001$).

I compared adult aggressiveness towards yearlings with that expressed towards other adults to determine whether adults treated yearlings differently than they treated other adults (Figs. 4.7 and 4.8). Only data from RG 1985 were used to calculate adult-adult interaction rates because it was the only colony-year in which adults were sampled using a "focal-scan" sampling regime. I assumed that patterns of adult aggressiveness for RG 1985 were representative of the patterns in other colonies and years. The patterns of aggressitivity between adult males and with other adult males, adult females, and yearlings all differed from one another (Fig. 4.7). Adult male-adult male agonism had two peaks, one early in the season during Periods 1, 2 and 3, and the other later in the season during Periods 5, 6 and 7 (Fig. 4.7). Adult males were less aggressive towards adult females than towards adult males with adult male-adult female aggression peaking during Period 2 and thereafter remained at a relatively low constant level until Period 8 when the rate dropped substantially, to the level at emergence (Fig. 4.7). Adult male-yearling agonism was high throughout the entire active season (except for Periods E and 1) peaking during Period 7 (Fig. 4.7). On average, adult

Fig. 4.7. Agonistic interaction rates of adult males towards adult males, adult females, and yearling Columbian ground squirrels over time. Data for adult-adult interactions are from colony RG (1985). Data for adult-yearling interactions from NFW, NFE, and RG, 1985 and 1986 combined. Females that bred as yearlings are excluded. Sample sizes for each interaction category are given above each time period. •————————• Adult male-yearling, •-------• Adult male-adult male, •··········• Adult male-adult female.

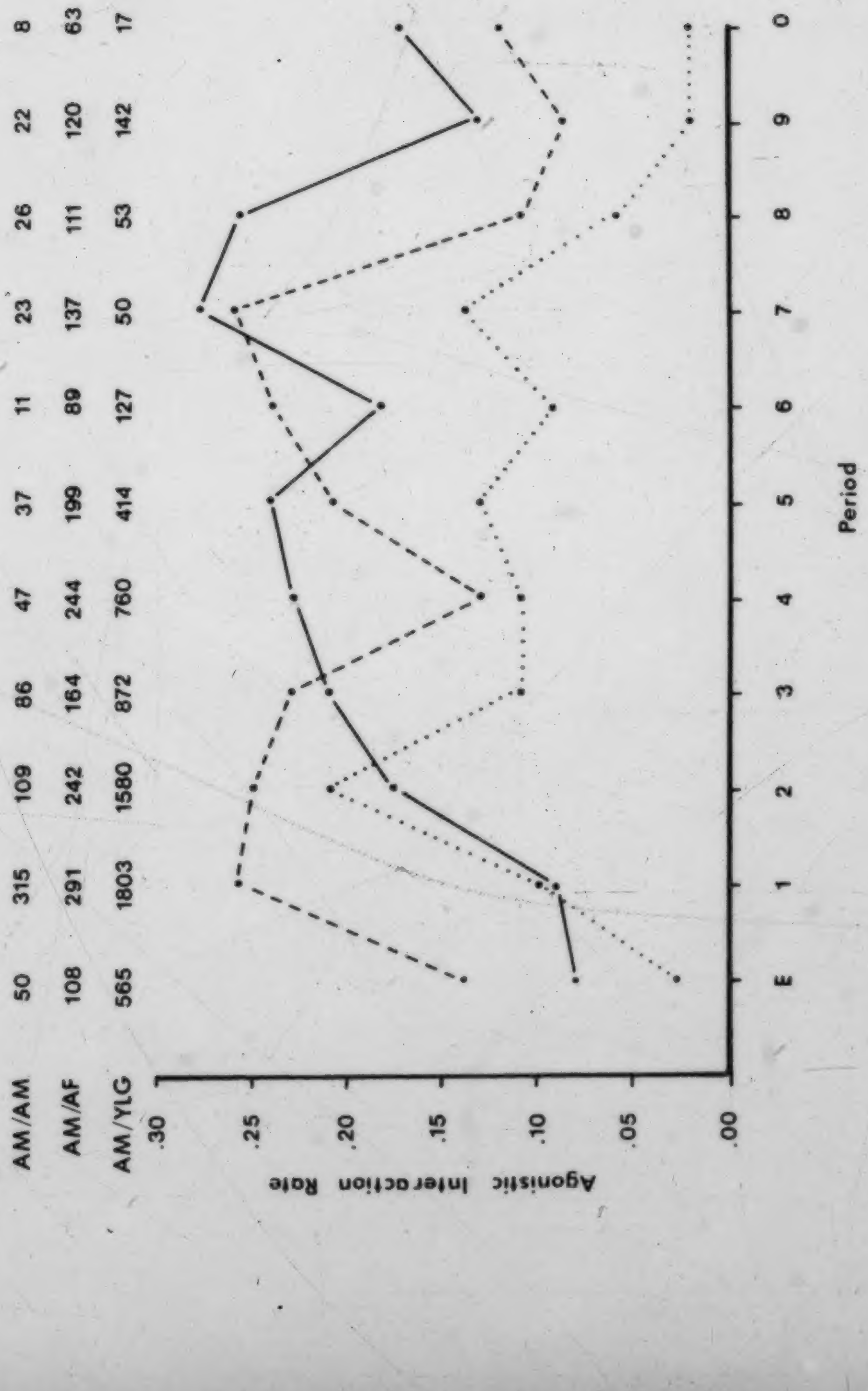
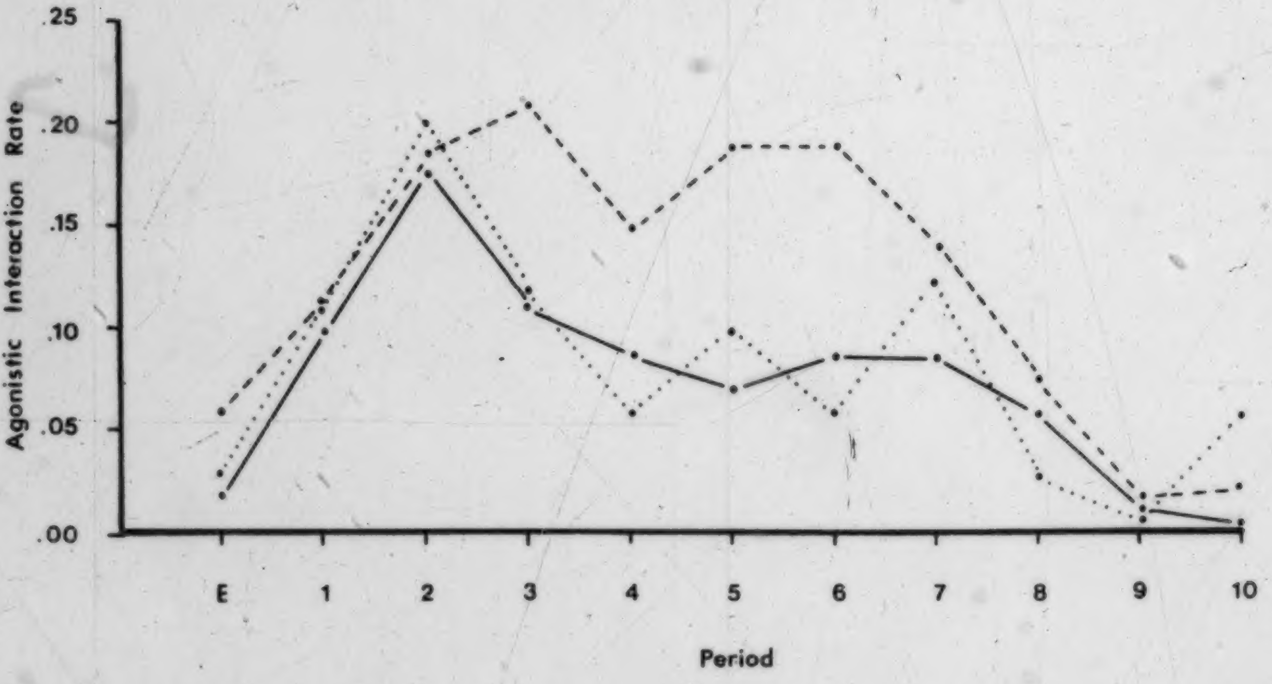

AM/AM 50 315 109 86 47 37 11 23 26 22 8
AM/AF 108 291 242 164 244 199 89 137 111 120 63
AM/YLG 565 1803 1580 872 760 414 127 50 53 142 17
Agonistic Interaction Rate
.30
.25
.20
.15
.10
.05
.00
E
1
2
3
4
5
6
7
8
9
0
Period

Fig. 4.8. Agonistic interaction rates of adult females towards adult males, adult females, and yearling Columbian ground squirrels over time. Data for adult-adult interactions are from colony RG (1985). Data for adult-yearling interactions from NFW, NFE, and RG, 1985 and 1986 combined. Females that bred as yearlings are excluded. Sample sizes for each interaction category are given above each time period. •– – – – – –• Adult female-yearling, •————• Adult female-adult male, •·········• Adult female-adult female.

AF/AM	70	187	179	135	242	197	71	111	96	84	32
AF/AF	49	188	173	88	216	212	100	137	121	149	33
AF/YLG	1163	1818	1834	1183	1942	1135	405	175	145	338	65



males were most aggressive towards other adult males (average agonistic interaction rate = 0.22), less so towards yearlings (0.16) and least toward adult females (0.11).

By contrast, adult females were more aggressive towards yearlings than they were towards other adults (Fig 4.8). On average, the adult female interaction rate with adult males was 0.09, with adult females 0.09, and with yearlings 0.15. The agonistic behaviour of adult females towards adult males and females peaked during Period 2, was relatively low and stable during Periods 3 to 7 and declined during Periods 8, 9 and 10 (Fig. 4.8). Adult female-yearling agonism was high during Periods 2 to 7 especially so during parturition (Periods 2 and 3) and juvenile emergence (Periods 5 and 6) (Fig. 4.8). It appeared that adult females treated adults and yearlings differently with the latter being involved in disproportionately more agonistic interactions (Fig. 4.8).

For the most part mothers were not involved in any more or less aggressive or cohesive interactions toward yearling sons and daughters than toward yearling nonoffspring (Fig. 4.9 and Table 4.3). The only exceptions were during Period 3 when the agonistic interaction rate between mother and son was lower and between mother and daughter was higher than between "unrelated" adult females and yearlings (Fig. 4.9). The large fluctuations in interaction rate between mother and sons beginning in Period 6 probably reflected small sample sizes. A difference of one or two interactions when sample sizes are low (1-20) drastically altered the interaction rates recorded (Fig 4.9).

Yearling-yearling interactions

Yearling males played significantly more often with other yearlings than did yearling females during Periods 1 to 4 (Fig. 4.10a). Although the frequency of play differed between the sexes, the patterns of play frequency over time were similar for both male and female yearlings (Fig. 4.10). For both sexes play was most frequently observed during Period 1. Thereafter the frequency of play declined slowly to Period 4 and then more rapidly to low levels during Period 6 (dispersal, juvenile emergence); thereafter, play was never recorded

Fig. 4.9. Comparison of agonistic interaction rates of mothers towards yearling sons and daughters with rates of agonistic interaction of adult female Columbian ground squirrels towards yearling-aged nonprogeny. All colonies (NFW, NFE, and RG) and years combined (1985 and 1986). Females that bred as yearlings are excluded. Sample sizes for each kin category are given above each time period. P = progeny (mother-son, mother-daughter), NP = nonprogeny. For both male and female yearlings •————• = P, •– – – – – –• = NP.

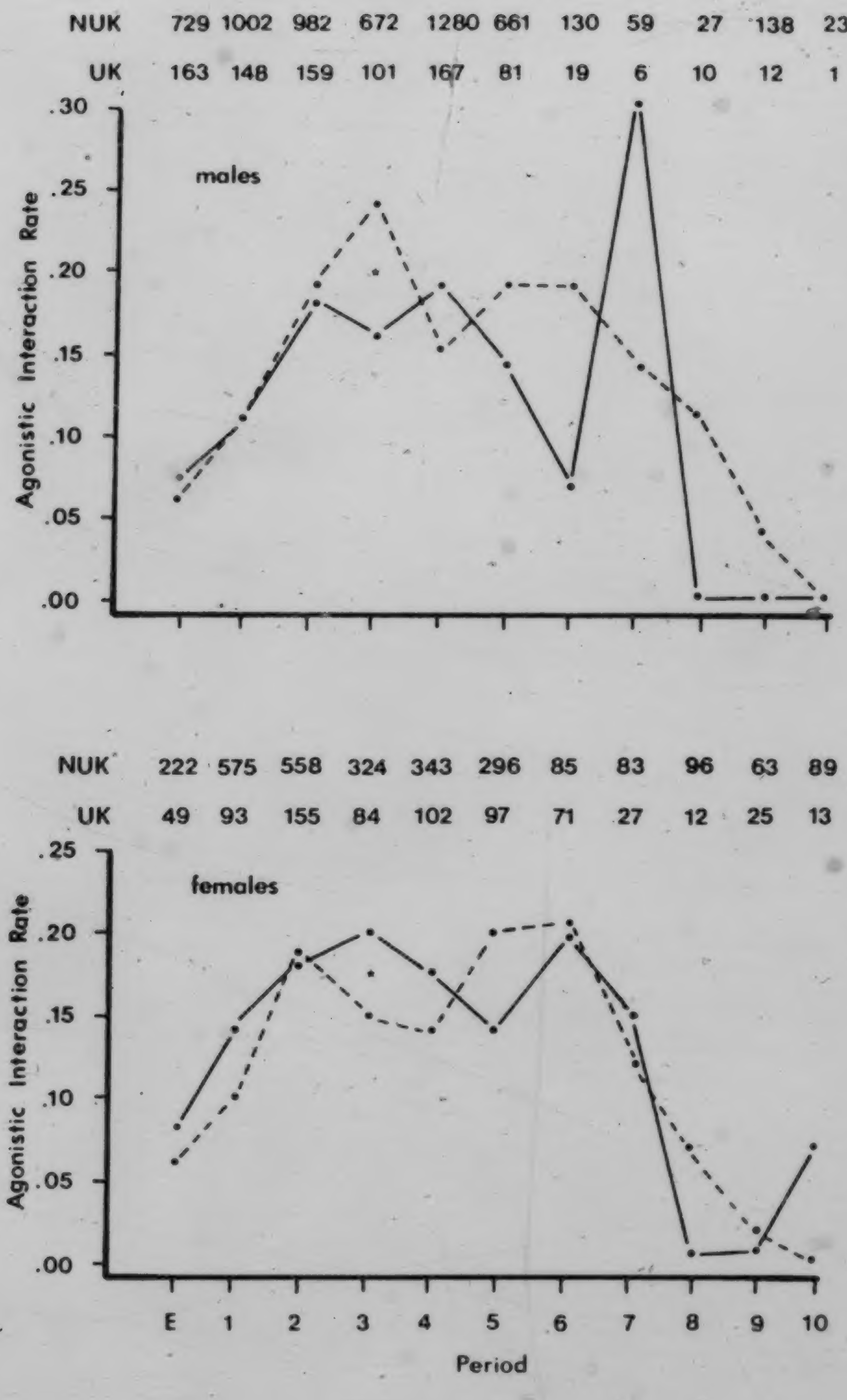
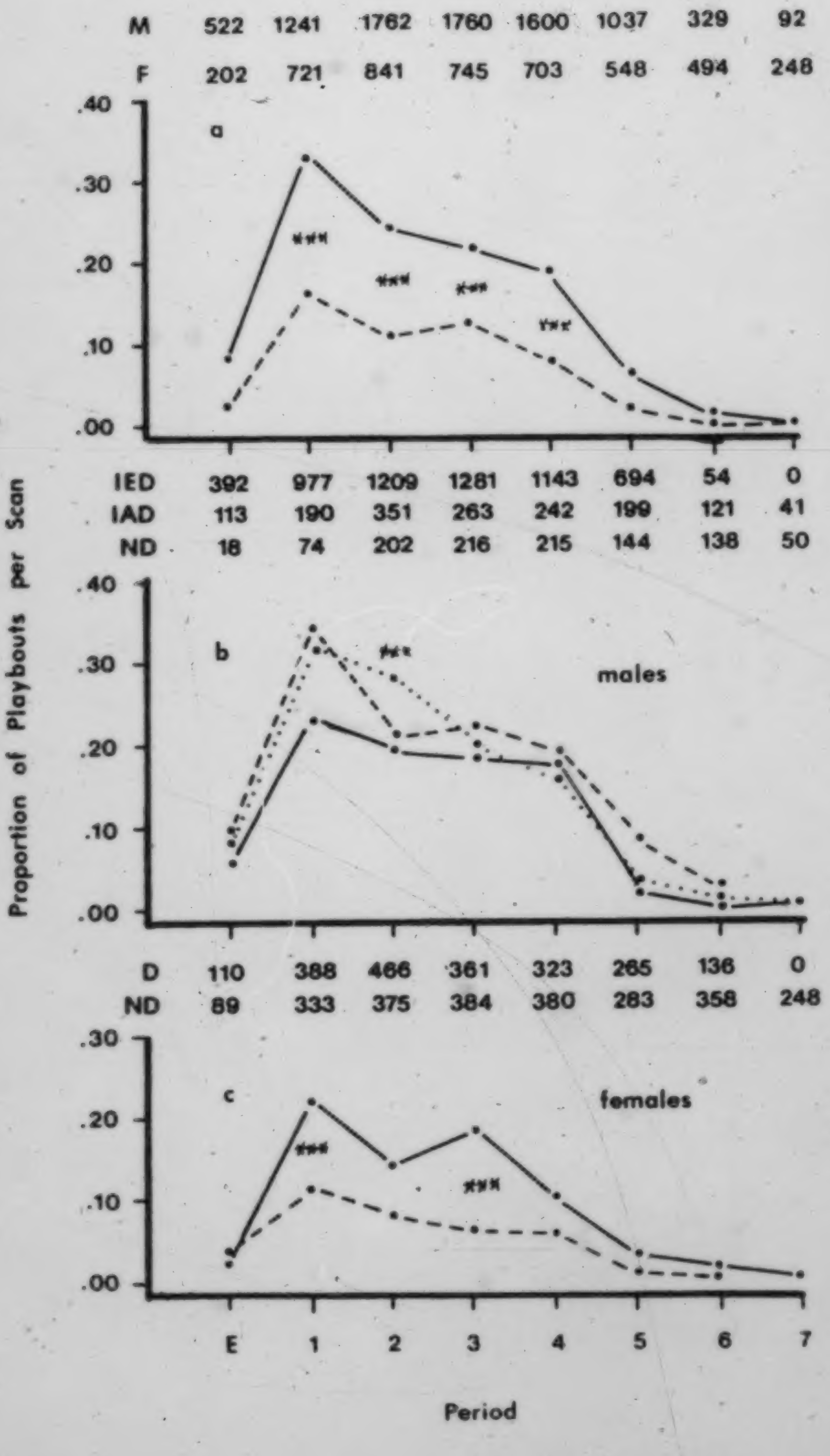

NUK 729 1002 982 672 1280 661 130 59 27 138 23
UK 163 148 159 101 167 81 19 6 10 12 1
males
.30
.25
.20
.15
.10
.05
.00
Agonistic Interaction Rate
NUK 222 575 558 324 343 296 85 83 96 63 89
UK 49 93 155 84 102 97 71 27 12 25 13
females
.25
.20
.15
.10
.05
.00
Agonistic Interaction Rate
E 1 2 3 4 5 6 7 8 9 10
Period

Table 4.3 Comparison of cohesive interaction rates (to period 6) among Columbian ground squirrels between mothers and yearling sons and daughters, versus adult females and yearling nonprogeny. All colonies (NFW, NFE, and RG) and years (1985,1986) combines. Excludes females that bred as yearlings. Number of spatial-temporal overlaps are given in parentheses.

Males			Females		
Mother	Non-Mother	Difference[1]	Mother	Non-Mothers	Difference[1]
0.03 (821)	0.02 (5348)	$P > 0.05$	0.03 (705)	0.02 (2905)	$P > 0.05$

[1] Chi^2 test

Fig. 4.10. Frequency of play bouts for yearling male and female Columbian ground squirrels, and nondispersers and dispersers over time. Data from colonies NFW, NFE, and RG and years 1985 and 1986 com~~bined. Females~~ that bred as yearlings are excluded. Sample sizes for each sex or dispersal category are given above time periods. Sexes: •————————• = males(M), •– – – – – –• = female(F). For males •————————• = nondispersers (ND), •·········• intracolony dispersers (IAD), •– – – – – – –• intercolony dispersers (IED). For females, •————————• = nondispersers (ND), •– – – – – – – –• dispersers (D). *** = $P \leq 0.001$. (X^2 test).


M 522 1241 1762 1760 1600 1037 329 92
F 202 721 841 745 703 548 494 248
.40
.30
.20
.10
.00
a
***
***
***
***
IED 392 977 1209 1281 1143 694 54 0
IAD 113 190 351 263 242 199 121 41
ND 18 74 202 216 215 144 138 50
.40
.30
.20
.10
.00
b
***
males
D 110 388 466 361 323 265 136 0
ND 89 333 375 384 380 283 358 248
.30
.20
.10
.00
c
***
***
females
E
1
2
3
4
5
6
7
Period
Proportion of Playbouts per Scan

among yearlings.

Only during Period 2 did yearling male nondispersers, intracolony and intercolony dispersers differ in the relative frequency of play observed (Fig. 4.10b). For Periods E to 6 combined the average frequency of play for yearling male nondispersers (0.14), intracolony (0.20), and intercolony dispersers (0.21) were significantly different ($X^2 = 25.814$, $P \leq 0.001$). Thus nondispersing male yearlings played less frequently with other yearlings than did their dispersing counterparts.

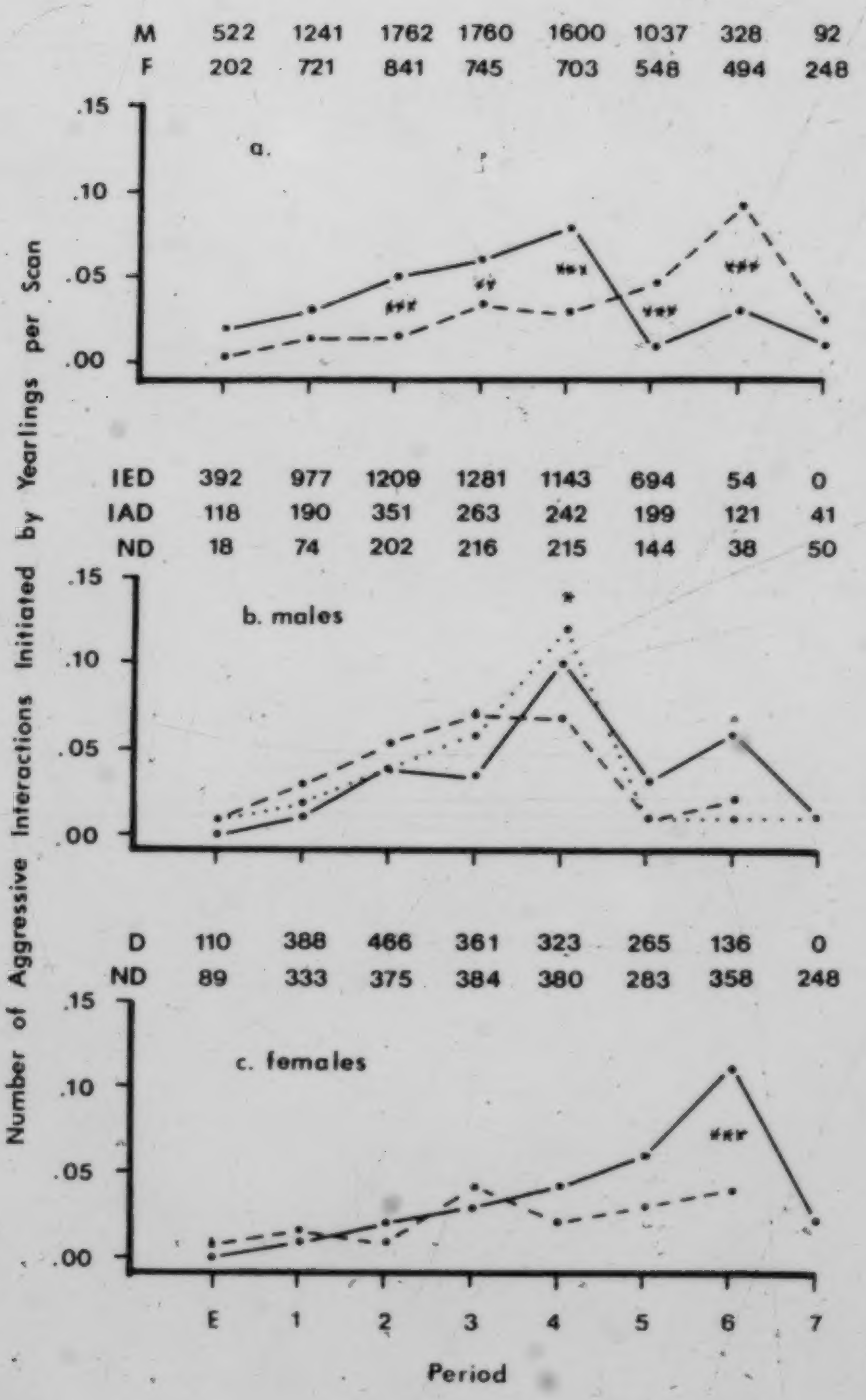
Among yearling females the opposite appeared to be true (Fig. 4.10c); nondispersers played more frequently than did dispersers, significantly more so during Periods 1 and 3. The frequency of play for yearling female nondispersers over Periods E to 6 was 0.11, significantly different ($X^2 = 31.0$, $P \leq 0.001$). than that for yearling female dispersers (0.06).

The frequency of initiation of aggressive interactions by yearlings towards other yearlings differed for males and females (Fig. 4.11a). Differences occurred not only in the amount but also in the pattern of aggressive frequency. Male aggressiveness towards other yearlings rose steadily to a peak in Period 4 and declined rapidly thereafter whereas female aggressiveness peaked during Period 6, and was low thereafter (Fig. 4.11a).

Among male yearlings, relatively little difference was recorded in the frequency of initiation of aggressive interactions between nondispersers, intracolony dispersers and intercolony dispersers (Fig. 4.11b). Only during Period 4 were the differences significant; intercolony dispersers initiated aggression towards other yearlings less frequently than did either nondispersers or intracolony dispersers (Fig. 4.11b). Among females, nondispersers initiated aggressive interactions more frequently than did dispersers at the peak of female aggressiveness (Period 6 - Fig. 4.11c) and over the Periods E to 6 as a whole (nondispersers = 0.11, dispersers = 0.06, $X^2 = 31.0$, $P \leq 0.001$).

Dominance relationships were determined for yearlings of the same sex within the same communal area. Yearlings were ranked according to their relative dominance status within the communal group as determined by the outcome of aggressive interactions. Among

Fig. 4.11. Number of aggressive interactions initiated per scan for yearling male and female Columbian ground squirrels, and for yearling nondispersers and dispersers over time. Females that bred as yearlings are excluded. Sample sizes for each sex or dispersal category are given above time periods. Sexes: •————————• = males(M), •– – – – – – • = females(F). For males: •————————• = nondispersers (ND), • · · · · · · · · • = intracolony dispersers (IAD), •– – – – – – –• = intercolony dispersers (IED). For females: •————————• = nondispersers (ND), •– – – – – – • dispersers (D). * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$. (X^2 test).


M 522 1241 1762 1760 1600 1037 328 92
F 202 721 841 745 703 548 494 248
a.
IED 392 977 1209 1281 1143 694 54 0
IAD 118 190 351 263 242 199 121 41
ND 18 74 202 216 215 144 38 50
b. males
D 110 388 466 361 323 265 136 0
ND 89 333 375 384 380 283 358 248
c. females
.15
.10
.05
.00
***
**
*
E 1 2 3 4 5 6 7
Period
Number of Aggressive Interactions Initiated by Yearlings per Scan

yearling males nondispersers ranked among the most dominant; intercolony dispersers among the least dominant (Table 4.4). Among five sibling-pairs that contained one nondispersing and one dispersing brother, the nondispersers "won" the majority of aggressive encounters with their brothers (33 of 50 interactions (66%)). Thus, it appeared that the most dominant males tended to remain on or near the natal home range and communal area while the less dominant males dispersed elsewhere (either within or beyond the natal colony).

Yearling female nondispersers and dispersers did not differ in their relative dominance ranks within the communal group (Table 4.4). Some very dominant as well as some very subordinate females dispersed or disappeared from the natal colony. Among the 3 sibling-pairs that contained one nondispersing and one dispersing sister, the nondispersers "won" more aggressive encounters than did the dispersers in all 3 cases (21 of 32 encounters (66%) were won by the nondispersers).

Discussion

The conspecific aggression hypothesis could not be rejected as a proximal cause of dispersal for yearling Columbian ground squirrels in this study. Evidence suggested that agonism from adult male, female, and yearling conspecifics were all factors that were correlated with the emigration of yearlings in this study. The timing of dispersal coincided with peaks of aggressiveness in adult male and female conspecifics. In some situations philopatric and dispersing yearlings were treated differently by adults; in such cases, nondispersers always received lower rates and/or frequencies of agonism than did dispersers. As well, nondispersers apparently avoided encounters with aggressive adults more successfully than did dispersers. Among yearling males dispersal was correlated with dominance - the most dominant males remained philopatric while the least dominant males dispersed. These data suggest that conspecific aggression may be the proximate stimulus prompting dispersal by yearlings in the Columbian ground squirrel, provided they have achieved sufficient body reserves by the time they are subjected to the high levels of agonism (Chapter 5).

Table 4.4 Mean dominance rank of yearling male and female Columbian ground squirrels that were nondispersers and dispersers and lived together on yearling communal areas. Females that bred as yearlings excluded. Sample sizes are given in parentheses.

	Nondispersers	Intracolony dispersers	Intercolony dispersers	Difference[1]
Male	3.8 (7)	4.4 (12)	4.9 (48)	$P \leq 0.05$
Female	1.9 (9)	-	1.9 (14)	$P > 0.05$

[1] Chi^2 test

Adult male-yearling interactions

In this study adult males interacted extensively and often intensively with yearlings of both sexes. Both the aggressive and cohesive interaction rates between adult males and yearlings were higher than the interaction rates between adult females and yearlings (compare Figs. 4.1 and 4.2). This observation was unexpected since others have reported that adult male-yearling aggression in Columbian ground squirrels was infrequent and occurred at lower levels than expected by chance (Festa-Bianchet and King 1984, Hackett 1987). Murie and Harris (1978) reported that agonism between adult male Columbian ground squirrels and other adults was confined mostly to the breeding season. After breeding, adult males apparently interacted infrequently with other conspecifics of any age. In this study adult males were aggressive towards all conspecifics and rates of aggressive interactions were high even outside the breeding period (Periods E and 1; Fig. 4.7).

There are at least two reasons why the interaction rates that I recorded between adult males and yearlings were higher than those previously recorded for Columbian ground squirrels. First, in this study I used all aggressive behaviours to calculate agonistic interaction rates whereas others (Murie and Harris 1978, Festa-Bianchet and Boag 1982, Festa-Bianchet and King 1984, Hackett 1987) used only chases in their calculations. Nevertheless, 81% of all aggressive interactions I recorded had chases as components of the interaction sequence. Even if the adult male-yearling interaction rates that I recorded were reduced by 19% they would still be high relative to the rates recorded by others (ie. Table 4 in Festa-Bianchet and King 1984).

Probably the single most important reason for the discrepancy in interaction rates between this study and others has to do with the calculation of interaction rates. Previous researchers have usually measured interaction rate on the basis of hours observed (Appendix 4). For instance Festa-Bianchet and King (1984) measured interaction rate as the number of chases per individual per hour and Hackett (1987) calculated interaction rate as the number of chases observed per hour. Such measures of interaction frequency do not take into account the availability of animals with which to interact (Michener 1980, Appendix 4). For instance, high frequencies of interaction early in the season (eg. during breeding) may occur because animals encounter each other more frequently earlier than later in the season (as in Figs. 4.5 and 4.6). Low frequencies of interaction do not necessarily mean that individual animals are any less aggressive than previously, but rather, that they are simply encountering each other less often (Figs. 4.5 and 4.6). Past research has emphasized the number of interactions seen and when this number was low, animals were usually assumed to be less aggressive. My data suggest that on a per encounter basis adult males are highly aggressive toward yearlings of both sexes and that this aggressiveness is distributed over a large portion of the active season (Fig. 4.1).

In 2 of the 3 years of their study, Festa-Bianchet and King (1984) found that adult male Columbian ground squirrels were more aggressive towards yearling males than towards yearling females. Downhower and Armitage (1981) reported that adult male yellow-bellied marmots (*Marmota flaviventris*) initiated more agonistic interactions with yearling males than with yearling females. Since adult males were not as closely associated in space with yearlings in the Festa-Bianchet and King (1984) study as they were in this study (Chapter 3), it is not surprising that these authors recorded low rates of adult male-yearling interaction especially when these rates were based on hours of observation and not numbers of encounters.

Since both Downhower and Armitage (1981) and Festa-Bianchet and King (1984) calculated interaction rate on the basis of number of interactions observed per hour, their interaction "rate" is really an interaction frequency and thus their data only suggest that adult males interacted more frequently with yearling males than with yearling females and not that adult males were more agonistic towards yearling males than towards yearling females on a per encounter basis. Yearling males may be chased more frequently because they make more extensive excursions than yearling females (Holekamp 1984) and thus have a greater chance of encountering adult conspecifics. Whether or not adult males are selectively aggressive towards yearling males can only be determined on the basis of per encounter comparisons between adult males and yearlings (Appendix 4). In this study yearling males were treated no more aggressively by adult males than were yearling females but females were treated more cohesively than were yearling males.

I could find no information from other studies which suggested that adult males treat individuals that ultimately dispersed any differently than they treated nondispersers. In this study, levels of adult male agonism and cohesion were not different when interacting with yearling male nondispersers and dispersers (Fig 4.3 and Table 4.1). On the other hand, adult male aggressive interaction rates and frequencies were higher towards yearling female dispersers than towards yearling female nondispersers (Fig. 4.3). Although this difference in aggressiveness could be interpreted as being a stimulus for dispersal by yearling females, further evidence suggests that adult male aggressiveness was more likely to cause yearling male than yearling female dispersal. For instance, rates of intercolony dispersal of yearling males were positively correlated with the ratio of adult males to females; this relationship was weaker among yearling females (Chapter 6). As well, the rate of dispersal by yearling males from communal areas that had overlapping adult male neighbours was higher (0.91) than the dispersal rate from communal areas without adult male neighbours (0.67). No such difference in dispersal rates was noted for yearling females (females living in communal areas with adult male neighbours = 0.32) versus females without adult male neighbours (0.28). Finally, 2-year-old male adults were more aggressive towards male yearlings than were older adult males and dispersal of male yearlings from communal areas with only 2-year old adult neighbours tended to be higher (0.93) than with only older adult male neighbours (0.82). The only relationship between adult male aggressitivity (frequency of aggressive interactions) and yearling female dispersal was greater aggressitivity towards dispersers than nondispersers. Yearling male dispersal, on the other hand, was correlated with the absolute and relative densities of adult males.

Yearling female dispersers tended to be less social than their nondispersing counterparts. Dispersing females played significantly less frequently (Fig. 4.10) and tended to initiate fewer aggressive interactions with other yearlings (Fig. 4.11) than did female nondispersers. Possibly something about the behaviour of the "asocial" dispersing females stimulated a stronger aggressive response in adult males than was stimulated by the "social" nondispersing cohort. For yearling males, even though agonism from adult males was equivalent among both nondispersers and dispersers (Fig. 4.3). Among yearling males the thresholds of response to social pressure from adult males may differ among behavioural phenotypes; some individuals may require high levels of agonism before moving while others may move only after a single encounter (Armitage 1986).

Yearlings of both sexes apparently began to avoid encounters with adult males once the levels of adult male aggressiveness rose (Period 2; Fig. 4.1). The number of spatio-temporal overlaps between yearlings and adult males was high during Periods E and 1 when adult male aggressiveness was low (Figs. 4.1 and 4.5), but thereafter dropped rapidly (Fig 4.5). Despite extensive overlapping of home ranges among adult males and yearlings during Periods 1-5 (Chapter 3), the encounter rate between the two age groups remained low, possibly because yearlings attempted to avoid contact with the aggressive adult males. In fact, those yearlings that had the lowest rates of spatio-temporal overlap with adult males were the same yearlings that tended to remain on or near the natal area and/or to remain within the confines of the natal colony. Intercolony dispersers of both sexes had the highest levels of spatio-temporal overlap with adult males (Fig. 4.5). Yearlings that avoided contact with adult males to the greatest degree lived on communal areas that contained few or no overlapping adult neighbours and these were the yearlings (at least for males) that were the least likely to disperse (Fig. 4.5). Thus adult male agonism appeared to affect the space use of both yearling males and females, and yearlings of both sexes avoided encounters with all adult males.

Most ground squirrels of the genus *Spermophilus* disperse during their first active season as juveniles (Holekamp 1984). Normally in such species the adult male cohort is neither spatially nor temporally associated with the juveniles (Michener 1983, Holekamp

1984). Consequently adult males have little opportunity to interact with juveniles , and adult male agonism has rarely been implicated as a cause of dispersal in juvenile *Spermophilus* (Holekamp 1984). Among the marmots (*Marmota*) dispersal is often delayed until the young are 1 or 2-years old (Barash 1973, Webb 1981, Armitage and Downhower 1974, Johns and Armitage 1979, Holmes 1984). Thus, adult male marmots have the opportunity to interact with subadult cohorts. Agonism is often cited as the stimulus by which delayed dispersers are prompted to emigrate; for marmots aggressive interactions with adults appear to be important but yearling males appear to be more affected by adult male aggression than by adult female aggression (Downhower 1968, Armitage 1974, Armitage and Downhower 1974, Downhower and Armitage 1981, Webb 1981, but see Brody and Armitage 1986).

With regard to Columbian ground squirrels, Festa-Bianchet and King (1984) suggested that adult male agonism may play a role in forcing dispersal of yearlings but they emphasized that adult female agonism and yearling-yearling competition were probably the primary cause of dispersal among yearlings. Hackett (1987) did not discuss the role of adult male aggression as a factor promoting dispersal in yearlings, presumably because adult males and yearlings on his four study sites were not normally spatially associated and thus had little opportunity to interact (Hackett, person. comm.). In the colonies I studied adult males and yearlings often shared the same areas (Chapter 3) and had much opportunity to interact. Where the spatial attributes of the habitat and the social relationships of populations differ, the proximal stimulus to dispersal seems also to vary. Thus the proximate stimulus may not be necessarily "preprogrammed" and invariate.

Adult female-yearling interactions

Among adult female ground squirrels of the genus *Spermophilus* there are usually two peaks of maternal agonism during the annual cycle, one after breeding but before parturition, and the other during lactation just before juvenile emergence (McLean 1984). The pattern of adult female agonism towards yearlings in this study followed a similar pattern; agonism peaked during periods 2 and 3 and during Periods 5 and 6 (Fig. 4.2). The patterns of adult female agonism towards adult males and other adult females were similar but different from the patterns they showed towards yearlings (Fig. 4.7). Adult females may be less aggressive to other adults than to yearlings because of the uncertainty of the form reciprocation will take especially when an adult female is at or beyond the edge of her "territory" (Festa-Bianchet and Boag 1982). Adult female aggressiveness is probably induced by hormonal changes related to pregnancy and lactation as non-reproductive adult females do not behave aggressively (Hackett 1987) and reproductively active female yearlings behave like reproductively active adults (Festa-Bianchet 1981, person. obs.).

Maternal agonism apparently had an effect on the use of space of yearlings. Most ground squirrels in this study emerged from areas where hibernacula were concentrated (Appendix 10). After they bred females became aggressive (Shaw 1924, Festa-Bianchet and Boag 1982, Hackett 1987, and Figs. 4.2 and 4.8) and lived on fairly discrete home ranges (Festa-Bianchet and Boag 1982, Chapter 3) that they defended from other conspecifics including their own yearling offspring (Hackett 1987 and Fig. 4.9). Yearlings of both sexes were seen to travel onto their maternal home range only to be chased away by the mother. Adult females apparently did not tolerate yearlings or any other age/sex class of conspecifics on their maternal territories (Festa-Bianchet and Boag 1982, Festa-Bianchet and King 1984, Hackett 1987); all intruders were chased away regardless of age, sex, or kinship (Figs. 4.2, 4.8, and 4.9). Maternal agonism apparently forced yearlings to live away from their natal home ranges and consequently on areas that were away from the mothers (usually the hibernacula area - Chapter 3). Festa-Bianchet and King (1984) reported that yearling *S. columbianus* moved to areas away from adult females when the frequency of female agonism peaked. Often yearlings moved to peripheral areas during peak agonism and returned to former areas after agonism had subsided (Festa-Bianchet and King 1984). Hackett (1987) reported that yearling *S. columbianus* were forced to live in the interstices around adult female home ranges once female agonism increased at the time of parturition.

In this study, maternal agonism may have been sufficient to cause dispersal of yearlings. The rate and frequency of adult female agonism towards yearling male nondispersers and dispersers was often significantly different (Fig. 4.4); nondispersers were chased at a lower rate or less frequently than were dispersers. As well nondispersers and dispersers usually differed in the frequency of spatio-temporal overlap with adult females; generally nondispersers encountered adult females at a lower frequency than did dispersers (at least prior to Period 7 - Fig. 4.6). Higher rates of encounter between yearling male dispersers and adult females resulted in higher frequencies of agonistic interactions with dispersers than nondispersers. On a per encounter basis, male dispersers were involved in aggressive interactions proportionally more often than were nondispersers (Fig. 4.4).

Since nondispersing male yearlings ranked higher in dominance status than dispersing males and females, and since nondispersing female yearlings were more "sociable" than their dispersing counterparts, nondispersing yearlings may have been more "confident" socially and elicited less agonism from adult females than did yearlings that ultimately dispersed. More frequent encounters that led to agonistic interactions with adult females may have caused less dominant and/or "asocial" yearlings to disperse while the more dominant and/or "social" phenotypes remained. Most dispersal occurred during the second peak of maternal agonism (Periods 5 and 6) which coincided with juvenile emergence (Chapters 2 and 3, Fig. 4.2). At the same time the aggressiveness among yearlings increased relative to earlier periods, with nondispersing yearlings initiating more aggressive interactions with other yearlings than did dispersing yearlings (Fig. 4.11). These social pressures against yearlings, including those incurred from adult males, together may have been enough to prompt dispersal of those yearlings that were physiologically susceptible to the pressure (Chapter 5). Aggressiveness from reproductively active females was apparently the first in a series of social "blows" against yearlings as this agonism (whether from the mother or the mother's neighbours) probably prevented yearlings from returning to their natal sites (Chapter 3).

Maternal agonism has been rejected as the proximal cause of dispersal among ground squirrels that disperse during their first active season as juveniles (Holekamp 1984). Among ground squirrel species that delay dispersal until their second active season (as yearlings) or later, agonism has been postulated to be the proximal cause of dispersal. For instance, Festa-Bianchet and King (1984) reported that dispersal of yearling *S. columbianus* coincided with the peak of adult female agonism, during late lactation. As well, these authors reported that yearlings that were chased most often by adult females (yearling males and certain groups of yearling male and female conspecifics) had greater rates of dispersal and disappearance than did yearlings that were chased less frequently. Hackett (1987) reported that no dispersal of yearling Columbian ground squirrels occurred on sites where adult females were removed or temporarily sterilized. As well dispersal of yearling males did not occur on reference sites if the mother was absent or did not become pregnant. Based on this evidence Hackett concluded that adult female agonism was sufficient to cause dispersal. Johns and Armitage (1979) proposed that the production of new litters by adult female yellow-bellied marmots (*Marmota flaviventris*) limited the extent to which their prior litters could delay dispersal. Holmes (1984) reported dispersal of subadult Alaskan Hoary marmots (*M. caligata*) whenever adult females reproduced. Brody and Armitage (1985) increased female philopatry and delayed male dispersal by removing adult females from a colony of yellow-bellied marmots. Thus, it is likely that maternal aggression also causes dispersal of prereproductive young in ground squirrel species characterized by delayed dispersal.

Yearling-yearling interactions

Festa-Bianchet (1984) and Hackett (1987) proposed that play behaviour and agonism among yearling Columbian ground squirrels may play a role in determining which yearlings ultimately disperse. Festa-Bianchet and King (1984) reported that male nondispersers ranked higher in dominance status than male dispersers in 1 of 3 years. In 1 year dominance relations could not be determined and in the other no differences in dominance status between male dispersers and nondispersers was evident (yearling female dominance relationships were not determined). Hackett (1987) reported that yearling females were dominant to yearling males and that yearling males remained on the natal area only in the absence of their sisters (and their mothers). Dispersal of female yearlings only occurred from multi-female litters, usually only the heaviest most dominant sister being able to remain on the natal area.

In this study yearling male nondispersers and intracolony dispersers were heavier and more dominant than intercolony dispersers (Chapter 5 and Table 4.3). Nondispersing males played less frequently than did dispersing males possibly because they were the most dominant yearlings of their sex and other males avoided playing or interacting with them. Pfeifer (1980) noted that juvenile male *S. elegans* that ultimately dispersed or disappeared initiated and received interactions from other juveniles significantly more often than did nondispersing males.

I found no evidence to suggest that nondispersing female yearlings were more dominant than their female dispersing counterparts (Table 4.3) except among the sibling pairs containing one nondispersing and one dispersing sister; the nondispersing sister was the dominant individual in all 3 cases. Of particular interest is the fact that of the nine litters containing at least two yearling sisters, in five cases (four litters of two, one of three) all remained on or adjacent to the natal site. Apparently resources were adequate on the natal sites to support both the mothers (none relinquished the natal site entirely to its daughters (*sensu* Harris and Murie 1984) and their two or three yearling daughters (all of which were present and brought young above ground the following year).

Unlike nondispersing male yearlings, nondispersing females played more frequently and initiated more aggressive interactions with other yearlings, making them appear to behave more "socially" than female dispersers (Figs. 4.10 and 4.11). Female dispersers were characterized by having significantly fewer female kin (mothers and sisters) in the natal colony than did nondispersers (Chapter 6). Rates of play among female nondispersers may have been higher than among dispersers because nondispersing playmates were often sisters

(King 1984, person. obs.)

Although maternal aggression was sufficient to cause movement of yearling offspring away from the natal site, it was not neccessarily sufficient to prevent their return after juvenile emergence. Female yearlings could usually only return to the natal site if their mothers were present (Chapter 6). Apparently once their juveniles had emerged most mothers tolerated those yearling daughters that had not dispersed but returned to the natal site (Chapter 6). Yearling females losing their mothers (removed (Chapter 5) or died overwinter) usually dispersed or disappeared from the natal colony probably because their former natal site had been taken over by other "unrelated" adult females that would not allow non-daughters to share a portion of their home range (Chapter 6).

No yearlings resided permanently on the communal areas which apparently were used only by yearlings (and adult males) to escape agonism associated with reproductively active females. Yearling females did not appear to compete with each other to remain on the communal area but rather usually attempted to return to their former natal site if the mother was still present (Chapter 6). Although there was some evidence to suggest that sisters competed to retain proximity to the natal area, often all sisters in a litter successfully established and reproduced on their natal home range. Inter-sibling competition among females to remain on the natal site has been documented previously for ***S. elegans*** (Pfeifer 1980) and ***S. columbianus*** (Hackett 1987).

Male yearlings also vacated the communal areas and attempted to return to the natal site, or moved to the periphery of the natal colony (Appendix 13), or dispersed from the natal colony altogether. The most dominant males remained within the natal colony and became established in vacancies, usually near the periphery. Presumably inter-male competition dictated which males remained and which dispersed from the natal colony (Chapter 5). Yearling males usually did not establish in the nearest vacancies available but moved an average of 3.2 vacancies before settling (Chapter 3). In Hackett's study male yearling Columbian ground squirrels were not spatially associated with other non-sib male yearlings and thus had relatively little opportunity to interact and form dominance relationships. Yearling males in Hackett's study were dominated by their yearling sisters and were usually forced to live elsewhere unless their sisters (and mothers) were absent.

General discussion

Differences in habitat structure result in differences in the spatial and social relationships among colonial Columbian ground squirrels in southwestern Alberta. On four colonies located on a large continuous meadow near Longview Alberta, Hackett (1987) reported that juveniles overwinter near their mother in hibernacula located within the natal home range. In the spring yearling siblings and their mothers shared space on the natal home range. An increase in maternal aggression around the time of parturition forced yearlings to move off the natal home range. Siblings competed for space on or near the natal site; usually only the most dominant sister remained while all other siblings dispersed. Dispersal occurred during the second peak of maternal aggression just before and during juvenile emergence. Adult males and "unrelated" (non-sibling) yearlings were not spatially associated with the yearling sib groups and apparently had little influence on yearling dispersal. In Hackett's study all pressure to disperse came from family members on the natal home range.

These observations contrast in many ways to those recorded on the three isolated meadows located near Turner Valley Alberta, where most squirrels hibernated in areas of good drainage and, because of prevailing winds, under accumulations of insulative snow cover (Chapter 3). Consequently, hibernacula were concentrated in several small areas within each colony. Mothers and yearling offspring usually emerged from hibernation in areas away from the natal home range. Once adult females had bred they returned to their former maternal home range or to the natal home range if first time breeders (Chapter 3). Adult females occupied relatively discrete non-overlapping territories. Yearlings appeared to try to return to the natal home range but were chased away by their aggressive pregnant mothers. Possibly to avoid maternal agonism yearlings "camped" on areas not used by adult females (usually the hibernacula areas). Adult males, also to avoid adult females, often lived with yearlings on communal areas (Chapter 3). Thus yearlings had to share space not only with their littermate siblings but also with "unrelated" yearling conspecifics and older more dominant adult males. Adult males were aggressive towards yearlings of both sexes but their agonism apparently affected yearling males more than yearling females as the proportion of males dispersing decreased in the absence of adult males. Yearling males competed for vacancies away from the communal area, usually only the most dominant (and heavy) males remaining within the natal colony. Yearling females, on the other hand, did not compete for space with non-sibling yearling females. Instead most yearling females with mothers present returned to their natal home ranges after juvenile emergence (Chapter 6). Sisters may have competed for space on the natal home range since in 3 cases dominant sisters remained while subordinates dispersed. Pressure to disperse for yearling females came mostly from family members (mothers and littermate sisters) and other adukt females whereas pressure to disperse for yearling males came not only from family members but also from adult males and "unrelated" yearling conspecifics.

Although the social structure and organization of squirrels in the two studies was different, a common denominator emerged; namely, in both studies maternal agonism was the initial factor promoting movements of yearlings. Once away from the home range interactions with siblings (Hackett's study) or with siblings, "unrelated" but neighbouring yearlings, and neighbouring adults of both sexes (this study), resulted in dispersal of yearlings both within and from the natal colony.

I have argued (Chapter 6), as have others (Hackett 1987 and citations therein) that maternal agonism is adaptive in that it increases female reproductive fitness through increased survival of offspring to independence (weaning). As a consequence of this maternal agonism, a female's previous young may be forced into a situation that ultimately results in their dispersal as yearlings. Dispersal may have fitness benefits for both the disperser and the dispersers close relatives (inclusive fitness benefits). For instance, a yearling male that disperses would no longer compete with its brothers or father for access to female mates. A male that fertilizes or attempts to fertilize the same females as its brothers or father is wasting much of its genetic potential (Smith 1979). As well, a male increases its inclusive fitness by mating with females other than his relatives (Dawkins 1978). Dispersal of offspring could prevent resource depletion on the natal area enhancing the future reproductive success of the mother and future offspring. The possibility of dispersing to areas rich in resources (burrows, food, and/or mates) could also greatly increase the fitness of dispersers.

In most mammals, females invest heavily in young and are the limiting sex; males invest relatively little and compete for access to females (Greenwood 1980). Females are more dependent on resources because of their heavy investment in young (Clutton-Brock and Harvey 1976, Packer 1979). The natal area is a proven area for the production of offspring and thus a female should benefit more by philopatry than males (Greenwood 1980), assuming adequate space and resources were available to meet their needs. One would expect females to compete to remain philopatric as part of their reproductive strategy (Pfeifer 1982, Hackett 1987). Female yearlings were dominant to male yearlings (Hackett 1987) and were more successful in re-establishing on the natal home range than were yearling males (Hackett 1987, and this study). Dominant female siblings apparently forced dispersal of less dominant brothers and sisters (Hackett 1987). Whether or not the dominant sister(s) were allowed to return and establish on the natal home range was contingent upon the presence and behaviour of the mother (this study). If resources are sufficient it would be advantageous for adult females to allow their daughter(s) to remain on the natal home range. The daughter(s) would avoid the costs associated with dispersal (Hackett 1987, Chapter 2) and would reap the benefits of philopatry (Waser and Jones 1983). Spatial and temporal overlap of females permits female kin clustering, nepotism, and cooperation to evolve (Sherman 1977, 1980, 1981, Michener 1983, Hoogland 1981, 1982, 1983a, b, 1986) and become an established part of the female reproductive strategy. Such a pattern would reinforce the need for males to disperse from their natal home ranges for the reasons outlined above.

Thus there is no need to invoke evolutionary hypotheses such as "inbreeding avoidance" (IA), "competition for mates" (CFM) or "competition for resources" (CFR) (see Dobson 1979, 1982, Greenwood 1980, Moore and Ali 1984, Liberg and Shantz 1985, Marks and Redmond 1987 for discussions) to explain the delayed male-biased dispersal of Columbian ground squirrels in southwestern Alberta. Natal dispersal of *S. columbianus* can just as easily be explained as a consequence of female reproductive strategies than as a consequence of IA, CFM, or CFR. This is not to deny that IA, CFM, or CFR play a role in dispersal but rather that these mechanisms probably evolved secondarily as a consequence of dispersal and presently contribute to the maintenance of the behaviour. For instance, once dispersal evolves (for whatever reason), populations will become more outbred and heterozygous. Inbreeding may then become costly (Bateson 1983, Ralls *et al.* 1986) and natural selection will operate to reduce these costs (ie. through reinforced male-biased dispersal or through behavioural avoidance of inbreeding - Hoogland 1982, Holekamp 1984, Cockburn *et al.* 1985).

As a consequence of dispersal males may reduce CFM with their close male relatives; males that disperse may gain greater inclusive fitness, reinforcing the benefits of dispersal by males. As a consequence of maternal agonism males may find themselves in areas of high male density (eg. as on communal areas in this study - Chapter 3). If under these circumstances a male is subordinate and unable to displace competitors, it may benefit by dispersing to areas of reduced male density (this study). Here CFM would reinforce dispersal even though the initial cause of movement away from the natal home range was a result of female reproductive strategy (maternal agonism). Along the same lines CFR could evolve as a secondary consequence of dispersal and reinforce the behaviour. I concur with Holekamp (1983) and Hackett (1987) that the greatest advances in our knowledge of the adaptive significance of dispersal will come first through an understanding of the proximal causes of the behaviour from which we can extrapolate more accurately to the ultimate level of causation.

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V. Weight Correlates of Natal Dispersal in Yearling Columbian Ground Squirrels

Intoduction

Correlates of weight have been hypothesized as the causal agents of dispersal in the small mammal literature (Gaines and McClenaghan 1980). Most hypotheses, for example, the "presaturation/saturation" hypothesis (Lidicker 1975), the "social subordination" hypothesis (Christian 1970) and the "genetic-behaviour polymorphism" hypothesis (Chitty 1967, Krebs 1978) predict dispersers to be socially subordinate and therefore light in weight relative to nondispersers (see Gaines and McClenaghan 1980 for a review). Contrary to these predictions, dispersal in most ground squirrels does not appear to be correlated with weight; that is, researchers have found no significant differences in weight between nondispersers and known or presumed dispersers (Slade and Balph 1974, Dunford 1977, Pfeifer 1980, 1982, Hackett 1987). Holekamp (1984a, b, 1986) reported that dispersing male Belding's ground squirrels (*Spermophilus beldingi*) were significantly heavier than were those that had not yet dispersed. Holekamp postulated that dispersal of juvenile male *S. beldingi* was triggered by the attainment of a critical body weight. In her study, all juvenile males eventually emigrated from the natal site and the timing of dispersal was correlated with attainment of a specific body weight; in other words, all males dispersed but only after a certain weight threshold was acheived. Holekamp (1986) suggested that this "ontogenetic switch" hypothesis be tested with other ground squirrel species.

Hackett (1987) has recently tested the ontogenetic switch hypothesis in Columbian ground squirrels. He noted that, unlike *S. beldingi* not all male *S. columbianus* dispersed from their natal sites (26% were philopatric); these philopatric males did not differ significantly in weight from males that dispersed. Moreover, the timing of dispersal was not correlated with weight - heavier animals did not necessarily disperse before lighter ones. In fact, among females heavier yearlings remained while lighter ones emigrated. Thus, Hackett rejected the ontogenetic switch hypothesis and concluded that dispersal of yearling Columbian ground squirrels was not triggered by attainment of a critical body weight.

Although emigration may not be *triggered* by achievement of a critical weight threshold, a minimum critical weight may still be necessary before an animal will undertake a dispersal movement (Baker 1978, Holekamp 1986). In other words, a threshold weight alone may not be enough to cause dispersal, but the achievement of a threshold weight may be a necessary prerequisite to dispersal. For example, some researchers have reported that particularily light weight or slow-developing individuals in some ground squirrel species are often the last to disperse or delay dispersal until the subsequent active season (Balph and Stokes 1963, Slade and Balph 1974, Festa-Bianchet and King 1984, Holekamp 1984b, 1986, Rayor 1985). Under these circumstances, emigration of individuals would occur only if the proximal stimulus for dispersal (eg. conspecific aggression, Chapter 4) is present *and* if the individual in question has reached sufficient weight to "afford" emigration.

The purpose of this chapter is to compare body weight and timing of dispersal in small isolated populations of Columbian ground squirrels in southwestern Alberta. Specifically, I test the "ontogenetic switch" hypothesis of dispersal and explore the possibility that a minimum body weight is required before dispersal will occur. As well, I discuss the ecological and evolutionary implications of correlates of body weight with dispersal.

Methods

Weight and dispersal data from three intensively studied sites (NFW, NFE, and RG - see Chapter 2 for descriptions) were used for the majority of the analyses presented herein. Where applicable, additional information was used from the other Category 1 (C1) and Category 2 (C2) colonies studied (see Chapter 2 for further details and descriptions). At each colony ground squirrels were individually identifiable through serially numbered eartags (one in each ear) and unique body dye-marks (Chapter 2). At NFW, NFE, and RG an attempt was made to recapture individual squirrels every 10 days. Trapping success varied but usually 80 to 100% of all animals present were recaptured each trapping round (Chapter 2). At each capture, age, sex, weight, reproductive status, and location of capture were recorded (see Chapter 2 for further details). A similar trapping regime was employed at the other C1 and C2 colonies studied except that at C2 colonies the trap rotation was longer (10 to 20 days) and recapture success during each trapping rotation was lower (60 to 80%).

The active season was divided into 11 ten-day intervals as outlined in Chapter 3. At each site these intervals were aligned to a common day. Day 60, the first day of period 6, was set to correspond to the median date of juvenile emergence at each colony. For analysis, weights of yearlings were compared on a standard day, eg. day 50. Known or estimated weight (weight based on interpolating weight values from individual growth curves - Hackett 1987) on a standard day was determined for individual yearlings. Day 50 was chosen as the standard day for comparison because it was the earliest day of dispersal (Chapter 3) and as well corresponded to a "standard date" used by Hackett (1987) in his weight analysis.

All terms used are those previously defined in Chapters 2 and 3. "Nondispersers" were yearlings that remained on or near their "natal site" and retained the same suite of neighbouring conspecifics. "Dispersers" were yearlings that permanently departed from both their natal site and their former neighbours. "Intracolony dispersal" refers to dispersal movements that occurred entirely within the confines of the natal colony whereas "intercolony dispersal" refers to movements between colonies (see Chapter 2 for a definition of "colony"). Confirmed intercolony movements were classed as "known intercolony dispersal" whereas disappearance of individual yearlings from the natal colony during the "dispersal period" was classed as "presumed intercolony dispersal" - see Chapter 2 for further discussion. The dispersal status of all yearlings present at NFW, NFE, and RG from 1984 to 1986 was determined as outlined in Chapters 2 and 3 and each yearling was classed either as a nondisperser, intracolony disperser, or known or presumed intercolony disperser. For individuals living in any of the other colonies studied, dispersal status could only be defined in terms of whether or not the yearling remained within or departed from the natal colony; eg. "colony philopatry" versus presumed or known "intercolony dispersal" (Chapter 2).

Statistical procedures follow those outlined in Sokal and Rohlf (1981) and Zar (1981). Parametric procedures were used only when distributions were normal and homoscedastic; otherwise nonparametric procedures were used.

Results

Since the mean weight of yearlings on day 50 in a given colony did not vary significantly among years (ANOVA; males $0.50>P>0.20$, females $0.20>P>0.10$), the data from within a colony were pooled among years. The ~~mean~~ weight of yearling males on day 50 differed among colonies, the heaviest males being recorded at RG and the lightest at NFE (Table 5.1). The weight of yearling females on day 50, however, did not differ among the three colonies (Table 5.1). At each colony yearling females were lighter than yearlings males on day 50 by 26 to 72g (Table 5.1).

At none of the three colonies studied did the mean weight of yearling males on day 50 differ significantly among the various categories of dispersers and nondispersers (Table 5.2). On the other hand, yearling female nondispersers, intra- and intercolony dispersers tended to differ in weight on day 50 (Table 5.3). When the data from the two categories of dispersers (intra- and intercolony dispersers) were combined, female dispersers weighed significantly more than nondispersers (Table 5.3).

The weight of individual yearlings of the same sex that occupied the same "communal" area (Chapter 3) was ranked, heaviest animals being ranked 1 with progressively lighter animals being ranked 2,3,4,5, etc. If two animals were the same weight on day 50 they were given equal ranks. All ranks were converted to a common scale of 10. Male nondispersers had a lower mean weight rank (ie. were heavier) than that of their dispersing or presumably dispersing communal conspecifics of the same sex (Table 5.4). By contrast, female yearlings that did not disperse had a higher mean rank (were lighter) than that of dispersers. Thus, it seemed that heavier males in a communal group were more likely to remain philopatric whereas heavier females tended to disappear (disperse).

Table 5.1 Mean ± SE (n) weight (g) on day 50 for yearling male and female Columbian ground squirrels at colonies NFW, NFE, and RG (1984-1986 data combined). Yearling females that bred were excluded.

	NFW	NFE	RG	Difference[1]
Male	510.4±5.9 (48)	484.0±7.8 (30)	535.0±8.9 (29)	$P \le 0.001$
Female	446.9±7.4 (32)	458.7±7.8 (23)	463.75±13.9 (8)	$P > 0.05$
Difference[1]	$P \le 0.001$	$P \le 0.001$	$P \le 0.001$	

[1] Based on ANOVA

Table 5.2 Mean ± SE (n) weight (g) on day 50 for yearling male Columbian ground squirrels that were either dispersers or nondispersers at colonies NFW, NFE, and RG (1984-1986 data combined).

	Nondispersers	Dispersers		Difference[1]
		Intracolony	Intercolony	
NFW	505.0±25.3 (2)	526.7±15.0 (12)	499.1±14.8 (34)	$\underline{P} > 0.05$
		506.3±5.9 (46)		$\underline{P} > 0.05$
NFE	493.3±15.5 (11)	502.5±13.1 (4)	485.3±8.7 (15)	$\underline{P} > 0.05$
		488.9±8.4 (19)		$\underline{P} > 0.05$
RG	510.0 (1)	560.0±16.7 (5)	530.8±23.6 (23)	$\underline{P} > 0.05$
		536.1±8.9 (28)		$\underline{P} > 0.05$

---

[1] Based on ANOVA

Table 5.3 Mean ± SE (n) weight (g) on day 50 for yearling female Columbian ground squirrels that were either dispersers or nondispersers at colonies NFW, NFE, and RG during 1984-1986 (all data combined).

		Dispersers		
	Nondispersers	Intracolony	Intercolony	Differe[illegible][1]
NFW/NFE/RG 1984-1986	445.9±7.2 (37)	443.3±38.5 (3)	467.8±5.8 (23)	$\underline{P} > 0.05$
		465.0±6.4 (26)		$\underline{P} \leq 0.05$

---

[1] Based on ANOVA

Table 5.4 Mean rank (n) on a weight scale of 1 to 10 for each sex among yearling male and female Columbian ground squirrels that were either nondispersers or dispersers and which were associated with the same "communal" group (Chapter 3). Includes data from 27 communal groups ($\bar{x}$ number of yearlings/group = 10, range = 2-17) located in colonies NFW, NFE, and RG during 1984-1986. Yearling females that bred were excluded from calculations.

	Nondispersers	Dispersers	
		Intracolony	Intercolony
Male	4.8 (12)	5.2 (23)	5.6 (85)
		5.5 (108)	
Female	6.7 (35)	6.7 (5)	5.3 (32)
		5.5 (37)	

Among sibling duos of the same sex, the heavier sibling dispersed in 2 of the 3 brother duos and in 1 of the 3 sister duos. These patterns run counter to the patterns observed in the communal groups but since the number of sib-pairs were so small these results must be viewed cautiously.

For both sexes of yearlings the estimated or actual weight at last sighting or capture of known and presumed intercolony dispersers varied widely (Fig. 5.1). Most males (78%) that dispersed (or disappeared) from the natal colony weighed between 480-590 g, but the range of weights of yearling males at the time of departure or presumed departure varied from 420 to 700 g (Fig. 5.1). Among females, the range of departure weights was smaller (420-610 g) possibly reflecting smaller sample sizes, and most females (88%) left the natal colony weighing slightly less than males (460-560 g - Fig. 5.1).

Although the departure weight of intercolony dispersers varied widely, individual yearlings apparently delayed dispersal until they were as heavy as possible. For example, the heaviest yearlings (based on day 50 weights) tended to be the first to disperse or disappear from the natal colonies (Tables 5.5 and 5.6) while lighter individuals dispersed or disappeared at a later date. Based on these observations one might predict that particularily lightweight individuals would delay dispersal until the following season when they were 2 years old. Only two 2-year-olds have ever been recorded dispersing between colonies (Chapter 2). Since both of these individuals (males) apparently dispersed during the regular "dispersal period" (Chapter 2), I assumed that all intercolony dispersal by 2-year-olds occurred during this time. Under this assumption I calculated rates of disappearance during the dispersal period for all 2-year-old natal residents inhabiting C1 and C2 colonies. In total only 8 of 61 (13%) 2-year-old males and 2 of 135 2-year-old females (2%) disappeared from their natal colonies during the dispersal period. Seven of the eight 2-year-old males that were presumed to be delayed intercolony dispersers came from 3 colonies (IO, BR, and JC - see Fig. 2.1 in Chapter 2). The eighth animal was an individual from DC (for details see Festa-Bianchet and King 1984). The weights of these 7 delayed "dispersers" as yearlings were estimated (or

Fig. 5.1. Final estimated or actual weight (g) of yearling male and female Columbian ground squirrels on the last day trapped or sighted in the natal colony. Data from colonies NFW, NFE, and RG and years 1984 - 1986 combined.

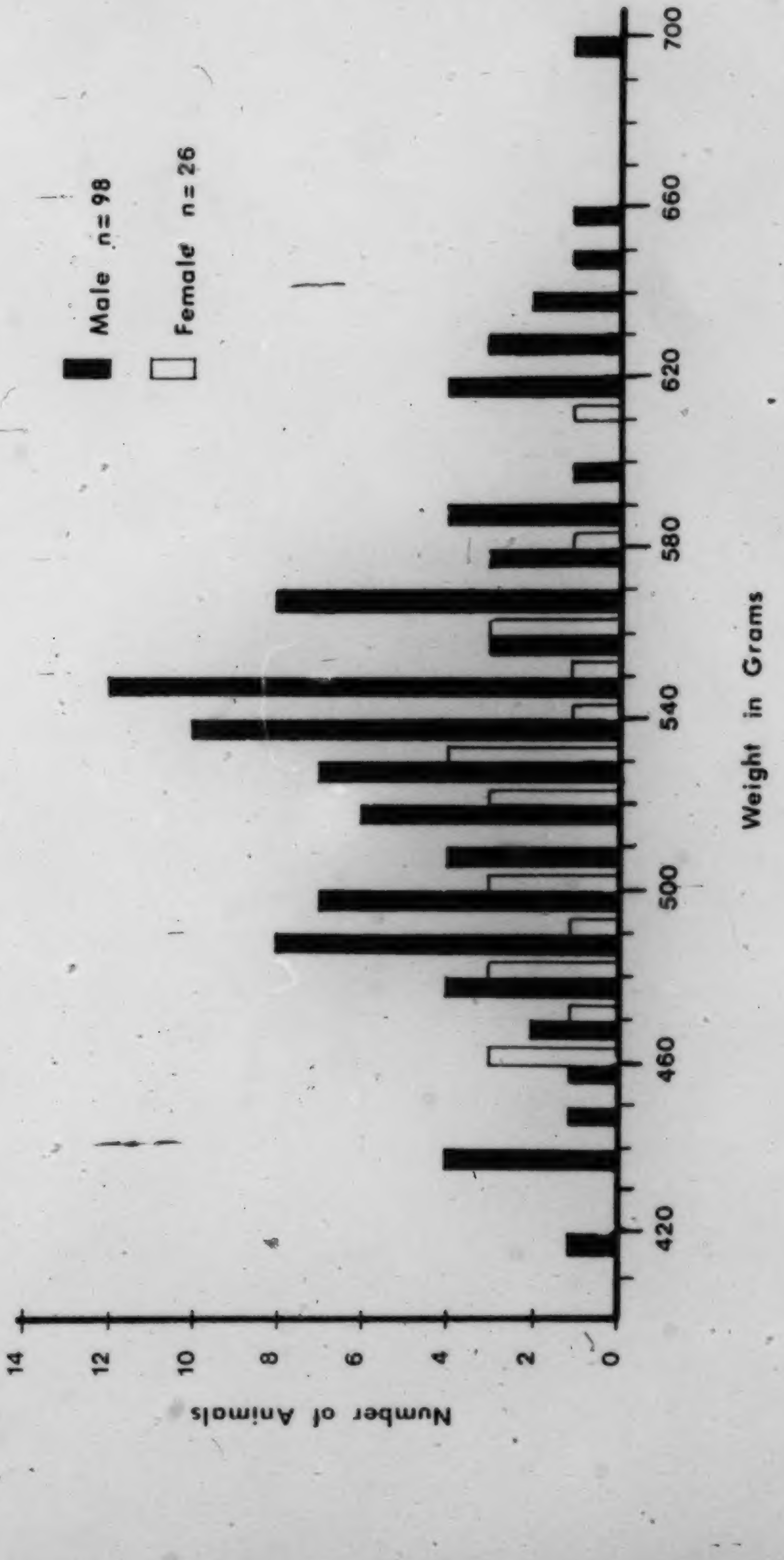
Male n= 98
Female n= 26
Number of Animals
0
2
4
6
8
10
12
14
420
460
500
540
580
620
660
700
Weight in Grams

Table 5.5 Mean ± SE (n) weight (g) on day 50 of yearling male Columbian ground squirrels relative to calander date of disapperance or dispersal from each of three natal colonies (NFW, NFE, and RG, 1984-1986 combined).

	NFW	NFE	RG
June 5-9	540.0±14.4 (5)	560.0 (1)	580.0 (1)
June 10-14	497.0±11.8 (15)	493.8±9.2 (13)	603.3±5.7 (3)
June 15-19	488.0±11.6 (15)	485.0±44.7 (2)	556.4±13.4 (13)
June 20-24	474.4±12.1 (9)	434.0±28.3 (5)	525.3±32.1 (3)
June 25-29	445.0±44.7 (2)	440.0±15.6 (3)	520.0±5.9 (3)
June 30- July 4			460.0 (1)

Table 5.6 Mean ± SE (n) weight (g) on day 50 of yearling female Columbian ground squirrels relative to calandar date of disappearance or dispersal from each of three natal colonies (NFW, NFE, and RG, 1984-1986 combined).

Date	NFW/NFE/RG
June 10-14	455.0±18.3 (3)
June 15-19	482.5±5.0 (2)
June 20-24	448.6±8.2 (7)
June 25-29	445.7±18.9 (8)
June 30-July 4	408.3±13.7 (5)

known) and were compared with the estimated (or known) weights of their yearling conspecifics that either disappeared or dispersed from their respective natal colonies as yearlings or remained philopatric to the natal colony as 2-year-olds. June 15 was chosen as a "standard date" to compare weights for these animals since the exact date of median juvenile emergence was unknown in each of ~~the~~ three colonies. Data from all three colonies over all years were pooled as there were no apparent differences in mean male weights on June 15 among colonies ($0.20 > P > 0.10$) or among years ($0.50 > P > 0.20$ - 2-way ANOVA). The seven animals that apparently delayed dispersal until age 2 years were significantly lighter as yearlings than both their conspecifics that apparently dispersed as yearlings and their conspecifics that ultimately remained philopatric as 2-year-olds (Table 5.7). The last group was the heaviest cohort.

The mean weights of yearling males and females during various "post dispersal" periods are given in Tables 5.8 and 5.9. Although sample sizes were small and incomplete data sets precluded statistical analyses, several trends are apparent; in 12 of 13 comparisons involving both sexes, intracolony dispersers of each sex weighed more than either nondispersers or intercolony dispersers. By contrast, intercolony dispersers weighed less than nondispersers or intracolony dispersers in 11 of 14 comparisons. Thus animals that made intracolony dispersal movements weighed more after dispersal than animals that had made intercolony movements. Had only nondispersers and "dispersers" been compared it is likely that no differences would have been apparent between the two groups in mean weight since the higher weights of the intracolony dispersers and the lower weights of the intercolony dispersers would have averaged out to the intermediate weights observed for nondispersers.

Discussion

Table 5.7 Actual or estimated weight (g) ± SE (n) on 15 June of male Columbian ground squirrels that presumably dispersed as 2-year-olds, and that remained in the natal colony[1].

Presumably dispersed as yearlings	Presumably dispersed as two-year-olds	Remained until immergence as two-year-olds	Difference[2]
439.2±11.0	397.1±16.7	471.4±10.7	$P \leq 0.005$
(13)	(7)	(7)	

---

[1] Data are pooled from colonies JC, IO, and BR, 1982-1985

[2] Based on ANOVA

Table 5.8 Mean (range) (n) weights (g) of yearling male Columbian ground squirrel dispersers and nondispersers during various post-dispersal periods at NFW, NFE, and RG.

	NFW			NFE		RG
	1984 (Period 9)	1985 (Period 9)	1986 (Period 6)	1985 (Period 8)	1986 (Period 7)	1986 (Period 6)
Nondispersers	-	-	530 (1)	662.5 (620-720) (4)	550 (500-600) (2)	540 (1)
Intracolony dispersers	760 (710-790) (3)	805 (740-860) (4)	536.7 (510-570) (3)	670 (1)	596.7 (570-620) (3)	576 (550-650) (5)
Intercolony dispersers	730 (1)	755 (730-780) (2)	505 (480-530) (2)	655 (560-760) (4)	540 (530-550) (2)	580 (1)

Table 5.9 Mean (range) (n) weights (g) of yearling female Columbian ground squirrel dispersers and nondispersers during various post-dispersal periods at NFW and NFE.

	NFW		NFE	
	1984 (Period 8)	1985 (Period 8)	1984 (Period 8)	1985 (Period 6)
Nondispersers	614.3 (560-690) (6)	543.3 (530-550) (3)	610 (3)	455 (400-510) (2)
Intracolony dispersers	680.0 (1)	-	640 (1)	-
Intercolony dispersers	580.0 (530-630) (2)	520.0 (1)	-	510.0 (1)

The Ontogenetic switch hypothesis

Holekamp (1984a, b, 1986) reported that juvenile male *S. beldingi* that dispersed were heavier than those of equivalent age (in days) that had not yet dispersed. She noted that all males eventually disperse and that the timing of dispersal was dependent upon reaching a critical body weight. Once a male reached the critical weight threshold it dispersed (but see Hackett 1987). Holekamp (1986) suggested that this "ontogenetic switch" hypothesis might apply to other ground squirrels but noted that the hypothesis could not explain polytypic dispersal behaviour among males that is, when they fell into one of two categories: "nondispersing" and "dispersing", unless a corresponding polymorphism in body mass or composition could also be demonstrated (Holekamp 1986 p. 385).

In the Columbian ground squirrel not all males disperse; a small proportion remain beyond the age of reproductive maturity on or near the area where they were born (Hackett 1987, Chapter 3). Thus for *S. columbianus* the ontogenetic switch hypothesis would predict polymorphism in yearling male body mass and that nondispersers weigh less than their dispersing counterparts. I found no significant differences in weight between males in the various dispersal categories (nondispersers, intracolony dispersers or intercolony dispersers) or between male nondispersers and dispersers (intra- plus intercolony dispersers - Table 5.2). Furthermore, when individual male yearlings that occupied the same communal area (Chapter 3) were ranked according to weight, nondispersers tended to outrank (outweigh) both intracolony and intercolony dispersers (Table 5.4). Thus heavier yearling males tended to be philopatric while lighter yearlings tended to disperse or disappear, the opposite of that predicted by the ontogenetic switch hypothesis. Hackett (1987) also reported that the weight for yearling male *S. columbianus* that dispersed did not differ from that of squirrels remaining on the natal area. Moreover, Hackett reported that yearling males dispersed at a wide range of weights with some particularily lightweight individuals dispersing while some very heavy individuals remained; his data do not suggest that dispersal occurred when males reached a critical weight threshold. I also recorded a great range of weights (420-700 g) on the presumed day of dispersal among yearling males on my three study sites (Fig. 5.2); for known intercolony dispersers, these weights ranged from 480 to 590 g.

Finally, if dispersal of male *S. columbianus* were triggered by attainment of a critical body weight, then one would predict that the timing of dispersal should vary with environmental and social factors that feed back on weight gain (eg. climatic variables, food quantity and quality, density, levels of aggression, etc.). The "ontogenetic switch" hypothesis would predict that the timing of dispersal should vary among years and between sites as a result of inherent interyear and intersite variability. Furthermore, the hypothesis predicts that dispersal could be relatively asynchronous, individuals leaving when they reached a critical weight which theoretically could occur at anytime during the summer period. Neither of these predictions held true for Columbian ground squirrels. Both Hackett (1987) and I found that the timing of dispersal at all sites studied was highly synchronous (Chapter 2 and 3) and that dispersal was always correlated with juvenile emergence no matter what the weight differences recorded between years and/or sites. The general synchrony of dispersal could not be explained by synchronous achievement by all males in all colonies of a critical "dispersal weight" because such did not occur (Fig. 5.2). Thus, the ontogenetic switch hypothesis is rejected as a presumed proximal cause of dispersal in male Columbian ground squirrels.

Holekamp did not apply the ontogenetic switch hypothesis to female *S. beldingi* since her hypothesis implicated a "sex-linked" mechanism involving only males. Nevertheless, Hackett (1987) tested the ontogenetic switch hypothesis on his yearling female *S. columbianus*. The predictions of the hypothesis were not upheld since Hackett reported that female yearlings dispersers were significantly lighter than those that remained. On the other hand, I found that female dispersers were significantly heavier than were their nondispersing counterparts. Why there was this apparent contradiction in our results are explored below. For now, my results for females appear to support Holekamp's contention that when dispersal is polytypic, there should also be a polymorphism in body weight; dispersers should be heavier than nondispersers as was the case for yearling females in this study. Furthermore, my data on females support another prediction of the ontogenetic switch hypothesis, namely that heavier animals should disperse before lighter ones (Table 5.6).

Although several predictions of the ontogenetic switch hypothesis were upheld for yearling female Columbian ground squirrels, further evidence suggests that the hypothesis is invalid. Yearlings of both sexes continue to gain weight throughout the summer but dispersal occurs only during a short period of time centered around juvenile emergence. In fact, the timing of female dispersal from the three colonies studied was more synchronous and of shorter duration than was male dispersal (Chapter 2). If dispersal were triggered only by achievement of a critical body weight why didn't the lighter weight female nondispersers disperse later in the season when their weights far surpassed the average weight acheived by dispersing females at the time of dispersal? The answer must be that body weight alone does not trigger dispersal. In sum, these results suggested that weight alone in *S. columbianus* did not initiate dispersal and therefore the ontogenetic switch hypothesis was rejected.

The results of other ground squirrel research support the contention that "dispersers" and "nondispersers" of either sex do not differ in weight and therefore dispersal could not possibly be triggered only by the attainment of a critical body weight. For instance, neither Slade and Balph (1974), nor Dunford (1977) nor Pfeifer (1980) found any significant differences in weight of dispersers (known and presumed) and nondispersers in *S. armatus*, *S. tereticaudus*, or *S. elegans*; Slade and Balph did note that "runts" seldom left the vicinity of the natal burrow. As well, Garrett and Franklin (in press) concluded that the physical condition of dispersers (based on body weight and wounding) was not different from that of residents in black-tailed prairie dogs (*Cynomys ludovicianus*). Thus, there seems to be little support for the predictions of the ontogenetic switch hypothesis. In fact, Hackett (1987) argued that Holekamp's weight analysis may be biased because she used post-dispersal weights in her comparisons of dispersers versus those that had not yet dispersed. Hackett reported that dispersing male *S. columbianus* benefitted from remarkable weight gains over their nondispersing conspecifics. Thus the differences in weight reported by Holekamp (1984a, b,

1986) for juveniles that had dispersed versus those still remaining on the natal site may have been the result of high rates of post-dispersal weight gain among those that had dispersed.

Weight as a prerequisite to dispersal?

Although my findings and the observations of others refute the idea that dispersal in ground squirrels is triggered by achievement of a critical weight, the possibility remains that weight may be a prerequisite to dispersal. Under the ontogenetic switch hypothesis weight is both necessary and sufficient to cause dispersal. Dispersal may occur, however, if a squirrel has sufficient energy reserves (in the form of fat) and if the initiating stimulus for dispersal (conspecific aggression - Hackett 1987 and Chapters 3, 4, and 6) is in place; in this case weight is necessary but not sufficient to cause dispersal.

Several lines of evidence support the view that the attainment of a certain weight is a prerequisite to dispersal. Among dispersers those individuals that dispersed or presumably dispersed first were the heaviest individuals followed by later departure of progressively lighter individuals. Individual yearlings may have to trade off between conflicting pressures; pressure to disperse from conspecifics (Chapters 4 and 6) versus a "reluctance" to disperse because of insufficient body mass or development. Lightweight individuals may "delay" dispersal a bit longer than heavier yearlings in favor of dispersing at a heavier weight in spite of agonism from conspecifics. There may be a physiological response to social pressure that combined with sufficient body weight (or development) manifests itself as emigration. Without pressure to disperse it does not matter what weight is achieved, emigration will not occur because the stimulus to disperse is not present. In this study, yearlings did not disperse after juvenile emergence even though great increases in weight were noted probably because conspecific aggression had subsided and no longer stimulated dispersal (Chapter 4).

The possibility that weight is a prerequisite to dispersal is further supported by the finding that males that presumably dispersed as 2-year-olds from the natal colony were significantly lighter as yearlings than were their counterparts that had dispersed or disappeared from their natal colony as yearlings (Table 5.7). Presumably these 2-year-olds had not reached sufficient body mass and physiological development to allow them to disperse as yearlings thus delaying dispersal until the following season. Interestingly, the heaviest cohort of yearling males remained within the natal colony as 2-year-olds. Thus, there were three categories of males; heavy weight nondispersers, medium weight dispersers, and light weight delayed dispersers.

The obvious question is why the differences in weight and dispersal status? Among yearlings there may be competition to remain on the natal area or to remain in vacancies elsewhere in the natal colony (Hackett 1987 and Chapter 4). Dominant individuals may outcompete subordinates for existing sites and thus subordinates may be forced to look elsewhere (Hackett 1987 and Chapter 4). Dominance is often correlated with weight; that is, heavy animals tend to dominate smaller ones. In this study, males that were philopatric (either to their natal site or natal colony) were apt to be heavier and more dominant individuals than their lighter dispersing or presumably dispersing counterparts (Table 5.4 and 5.7 and Chapter 4). Thus the heaviest yearlings could successfully procure vacancies in the natal colony while other lighter and less dominant yearlings (Chapter 4) were forced to leave the colony. Particularily lightweight yearlings although presumably pressured by aggressive conspecifics to disperse may not have emigrated because of insufficient body mass. As 2-year-olds the heaviest cohort probably retained their weight advantage and dominance over the lighter 2-year-olds. Since the lightweight 2-year-olds were much larger than they were as yearlings (Wiggett, unpubl. data), social pressure combined with sufficient weight may have initiated dispersal of this cohort. Of course, if no pressure to disperse from conspecifics was present, both light and heavy 2-year-olds would probably have remained in the colonies.

The above situation applies only to male and not female 2-year-olds. All female 2-year-olds whether heavy or light in weight showed signs of sexual maturity and breeding (see Chapter 2 for criteria). Females that breed did not disperse, none of the 60 yearling females known to have bred in six colonies dispersed from their natal home range or natal colony (Appendix 15). Thus delayed dispersal as a function of body weight could be tested only with males.

No 2-year-old male or female has ever been recorded dispersing or disappearing from NFW, NFE, or RG even though these colonies have been studied for 4,5, and 8 years respectively (see Table 2.1 and Chapter 2). If there was a minimum weight requirement for dispersal to occur, apparently all yearlings at these three sites always met the requirements since no delayed dispersal was recorded. On the other hand, at IO, JC, and BR delayed dispersal was fairly common; seven of 14 male 2-year-olds dispersed or disappeared during the dispersal period from these 3 colonies. Individual yearlings at IO, JC, and BR were much smaller on average than were yearlings at NFW, NFE, and RG (compare Tables 4.1 and 4.7). Squirrels emerged at IO, JC, and BR 2-3 weeks later than at NFW, NFE, and RG and consequently had shorter active seasons than the latter (time of immergence was similar among both sets of colonies), and had less time to grow and develop. A short active or growing season could result in delayed dispersal. For instance, *S. columbianus* populations in Washington have a longer above ground active season than do populations in southwestern Alberta (Murie pers. comm.). In Washington, Columbian ground squirrels apparently disperse as juveniles (Shaw 1924, Hackett 1987), presumably because the longer active season (=growing season) permits juveniles to obtain sufficient weight to disperse, become established and survive hibernation (Hackett 1987). Similarily, Festa-Bianchet and King (1984) postulated that dispersal is delayed until their second summer for Columbian ground squirrels in southwestern Alberta because of the relatively short first active season. They noted that juvenile *S. columbianus* spent only 45-55 days above ground at the colony studied (DC) and entered hibernation weighing much less (40-60% less) than adults. By contrast they reported that for *S. parryii* and *S. richardsonii* , which normally disperse as juveniles, the above-ground active season lasts for 80-120 days or more and that the juveniles are approximately 90% of adult size at immergence. Thus for Columbian ground squirrels dispersal may be delayed until they approach adult size - in southwestern Alberta that would be as yearlings, or in some cases as 2-year-olds (Boag and Murie 1981).

Evidence from other ground squirrel species support the idea that weight is a prerequisite to dispersal. Holekamp (1984a, b, 1986) found that heavier male *S. beldingi* disperse before lighter ones and that dispersal of some light weight males was delayed until the following spring when they were yearlings. Balph and Stokes (1963) and Slade and Balph (1974) noted that *S. armatus* "runts" were the last to leave the natal burrow and that these individuals seldom dispersed. Rayor (1985) found that male Gunnison's prairie dog (*C. gunnisoni*) that occupied a food-rich environment were heavier, more likely to disperse, and dispersed or disappeared at a younger age than did males that lived in an impoverished environment. Among marmots, those species that live at low elevations (eg. *Marmota monax*) tend to disperse as juveniles, those living at mid-elevations (eg. *M. flaviventris*) disperse as yearlings, while those species living at high elevation (*M. olympus*) tend to disperse as 2-year-olds (Barash 1973). Intraspecific differences in the age at dispersal are also evident among marmots; for example, yellow-bellied marmots (*M. flaviventris*) from low, mid or high altitude populations have been reported to disperse as juveniles (Webb 1981), yearlings (Armitage and Downhower 1974, Webb 1981) or 2-year-olds (Johns and Armitage 1979). Barash (1973) postulated that the age at dispersal in marmots is related to length of growing season and the weight of potential dispersers relative to adult body weight. Thus among the marmots, individual young apparently delay dispersal until a certain body weight or stage of physical development was reached; weight *per se* apparently did not initiate dispersal but rather appears to be a prerequisite for it.

Female weight comparisons

Hackett (1987) reported that the only instances of yearling female dispersal occurred from multi-female litters. Yearling sisters appeared to compete to remain on the natal area; generally only the heaviest, most dominant sister was able to remain philopatric while the other sisters dispersed. On the other hand, female nondispersers in my study were significantly lighter than were known or presumed dispersers and dispersal of all but one sister from my multi-female litters was uncommon. In only three of the nine litters that had two female siblings present as yearlings did only one sister remain while the other dispersed. In five of nine multi-female litters all sisters from a litter (four litters with two sisters, and one litter with three sisters) remained on or near the natal site. In only one litter did both sisters disperse. Dispersing yearling females were characterized by having few close female kin (eg. mother and/or sisters) present in the natal colony (Chapter 6); one half of dispersing females (8 of 16) had no mother present. Most females without mothers lost proximity of access to their former natal areas as other adult females were quick to take over vacancies. Many yearling females with few female kin (especially those without mothers) lived peripherally on communal areas. These females interacted little with other yearlings and seemed almost "asocial" (Chapter 4). Possibly because they interacted less and were more "peripheral" on the communal area, dispersers may have had more opportunity to acquire limiting food resources (more time feeding, less time interacting plus the benefits of less competition for food by living nearer to the edges of communal areas - Table 5.3). Dispersing females did not appear to be dominant to nondispersers although dispersers were significantly heavier than nondispersers. Possibly since dispersers were unable to compete with the adult females that usurped their former natal area (eg. they had no opportunity to inherit the mother's former home area - Harris and Murie 1984), and since they were unable to displace other yearling females, their only alternative was to disperse in order to find a suitable vacancy. In Hackett's (1987) study both dispersing and nondispersing yearling females had resided on the maternal home range (natal site). Thus both classes had to compete with their kin for access to food resources on the maternal home range. Unlike the situation in this study both nondispersers and dispersers in Hackett's study had equal opportunity to usurp (or inherit) a portion of the maternal home range; apparently the heaviest most dominant sister was usually the successful one. In my study, weight and dominance among "unrelated" yearling females appeared to be unimportant as only females with close kin (especially those with the mother present) could return to their former place of birth and subsequently hold space(Chapter 6).

Post Dispersal weight comparisons

Hackett (1987) noted that the post dispersal weights of yearling male nondispersers and dispersers were significantly different. Males that dispersed were as much as 100 g heavier by fall than were nondispersers. Hackett postulated that the additional weight gained by male dispersers was likely possible because they were able to escape from social pressure and competition for food by moving to peripheral areas of the colony where densities were much lower. In contrast Hackett found no post-dispersal weight differences between females that dispersed and those that remained on the natal area. He concluded that no weight benefit accrued to females that dispersed.

The post dispersal weights of yearlings on my three study sites showed the same pattern in both sexes, similar to that observed for males by Hackett (1987). Generally, intracolony dispersers of both sexes weighed the most, followed by lighter-weight nondispersers, and finally by even lighter weight intercolony dispersers (Table 5.8 and 5.9). Apparently the greatest cost in terms of subsequent weight gain was incurred by intercolony dispersers. Presumably the costs associated with moving relatively long-distances during dispersal as well as the costs associated with establishing in an unfamiliar colony (eg. high rates of aggression towards immigrants - Festa-Bianchet and King 1984, Wiggett unpubl. data) resulted in lower weight gain among intercolony dispersers. Nevertheless these costs did not appear to be very great; intercolony dispersers weighed less than nondispersers or intracolony dispersers but the differences were not great (Tables 5.8 and 5.9).

Intracolony dispersers appeared to suffer no weight costs whatsoever. Excursionary movements to the site where individual intracolony dispersers finally settled caused no measurable weight loss. Apparently such short distance movements are not energetically demanding. Most intracolony dispersers settled peripherally (Appendix 13) and in areas of lower density (Appendix 2), as Hackett found for his "dispersers". Intracolony dispersers subsequently had the greatest post-dispersal weights of all yearlings. Intracolony dispersers were subjected to aggressive interactions less often after their dispersal than before they had moved (Chapter 4) and also intracolony dispersers were interacted with agonistically less frequently after dispersal than were their nondispersing counterparts (Chapter 4). Thus the release from aggression and possibly reduced competition for food once intracolony dispersers moved may have resulted in the increased weight gains recorded.

Nondispersers suffered no weight costs associated with dispersal and/or establishment in an unfamilar area, but they may have had reduced weight gain because of competition for food on the higher density natal site or because of the higher rates of post-dispersal agonism encountered there (Chapter 4). Nondispersers had lower post-dispersal weights than intracolony dispersers but higher weights than intercolony dispersers. Although there appeared to be consistent weight differences between these three groups, the differences were not large, and successful dispersers certainly did not seem to suffer any great weight costs relative to nondispersers.

I am not certain why Hackett's female dispersers did not ultimately weigh more than their nondispersing counterparts after dispersal since his dispersing females also settled peripherally as did dispersing males. Prior to dispersal female "dispersers" on Hackett's areas weighed significantly less than "nondispersers" but after dispersal, as females reached their peak weights, dispersers and nondispersers weighed the same (Hackett 1987). Apparently some weight advantage did accrue to female dispersers since they managed to "catch up" with weights of the heavier nondispersers.

Theoretical considerations

The data from this study and from Hackett (1987) provide strong evidence against the operation of an "ontogenetic switch" (Holekamp 1984a, b, 1986) in prompting dispersal of yearling male and female Columbian ground squirrels. Our data refute the contention that acheivement of a critical weight threshold initiates dispersal. Contrary to predictions of the ontogenetic switch hypothesis, nondispersers were either heavier than dispersers (males in my study, females in Hackett's) or no differences were recorded (males in Hackett's study). Furthermore, the general synchrony in timing of dispersal and the wide range of weights at which yearlings dispersed or presumably dispersed provides strong evidence against body weight as a mechanism prompting dispersal.

At least two situations exist in which there would be no selective advantage for individuals to be stimulated to disperse upon achieving a specific weight threshold. In the first, probably very little selective advantage would accrue to an individual prompted to disperse from an area where resources and space were abundant (ie. as in newly established colonies). The animal in question would probably have no trouble reaching the critical weight threshold but would be leaving optimal habitat in return for the risks of dispersal (Chapter 2, but see Hackett 1987) and the presumed costs of settling in another colony (Festa-Bianchet and King 1984, Hackett 1987). By contrast, an individual born into a colony where densities are high and resources are limiting may gain a great selective advantage by dispersing (Lidicker 1975) but because of intraspecific competition for food and resources may not be able to reach the critical weight threshold required to permit dispersal. In both cases, the stimulus for dispersal acts in a manner that would probably reduce the individual's fitness. Achievement of a critical weight as a proximal cause of dispersal seems counterintuitive.

Holekamp (1986) has argued that the "ontogenetic switch" is the proximal stimulus that initiates dispersal and that dispersal of juvenile male Belding's ground squirrels "evolved to permit improved access to receptive females whose mate choice behaviour, in turn, evolved to minimize nuclear family incest" (p. 387). In other words, all males disperse in order to find "unrelated" females that will mate with them and the cue that initiates dispersal is weight-related. Precisely how weight as a cue to dispersal and ultimately as a cue to avoidance of close inbreeding evolved is an open question. Certainly body weight as a mechanism to prevent inbreeding avoidance is not a very parsimonious contention. One expects natural selection to act simply and directly; that is, if inbreeding avoidance were important then the cue most likely to cause dispersal should come from female kin as Hackett (1987) has postulated for Columbian ground squirrels. Certainly if female kin force dispersal of males to prevent inbreeding then the mechanism will be much more efficient in terms of individual (and inclusive) fitness benefits than if weight triggered dispersal. There is probably no selective advantage for males to disperse off the natal area in the absence of female kin as long as there are "unrelated" females nearby with which to mate. Body weight as a stimulus to prompt dispersal in order to prevent incestuous matings would result in "mistakes" ie., dispersal of males in the absence of female kin. As such, the mechanism is indirect and relatively inefficient and by virtue of its complexity would not be likely to evolve.

On the other hand, the idea that a minimum body weght is required before dispersal will occur has both empirical support and, in theory, strong selective advantages. Individuals will disperse only if the proximal cue to dispersal is in place and if the individual has sufficient resources in the form of fat to afford a dispersal movement. Natural selection would favour those individuals with the greatest energy reserves at the initiation of dispersal (Baker 1978). Individuals with low energy reserves may face greater risk of mortality in transit or greater risk of mortality during the following winter than those individuals with greater energy reserves. The data from this study supported the idea of weight as a prerequisite to dispersal; the heaviest animals dispersed or presumably dispersed first and were followed by progressively lighter individuals. In colonies with shorter active seasons (IO, JC, and BR) where individual squirrels had less time to grow and develop, the smallest individuals apparently delayed dispersal until they were 2-year-olds. In such situations it may be advantageous for exceptionally small individuals to delay dispersal even if the proximal stimulus to disperse (ie. conspecific aggression) is strong, especially if there is a significant energetic cost to emigration and subsequent establishment elsewhere. Although sample sizes are small, the preliminary data presented here suggest that there was a cost associated with long-distance dispersal. Intercolony dispersers had the lowest postdispersal weights of all yearlings. Nevertheless, the differences were not very large, intercolony dispersers usually only weighed, on average, about 5% less than intracolony dispersers and nondispersers (Tables 4.8 and 4.9). It is conceivable that intercolony movements are costly but that these costs are masked by great post-dispersal weight gains after settlement in the "new" colony. Certainly intracolony dispersers in this study and "dispersers" in Hackett's (1987) study gained weight advantages after dispersal. Unfortunately, I have insufficient data to determine whether or not such advantages accrue to intercolony dispersers. That there are costs and benefits to dispersal is a widely held assumption (Lidicker 1975); the goal for future research is to qualify and quantify these costs and benefits in order to determine the adaptive significance of dispersal.

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VI. Kinship and Demographic Correlates of Natal Dispersal in the Columbian Ground Squirrel

Introduction

In the ground squirrel literature, both kinship and demographic correlates of dispersal have been reported (see Holekamp 1984 for a review). Holekamp (1984) concluded that natal dispersal of male ground squirrels is density independent whereas that of females is density dependent. Holekamp also concluded that social factors such as aggressive interactions with kin, which under high population density in the natal area would be increased in frequency, were the probable causes of dispersal for young female ground squirrels. For males, Holekamp concluded that social interactions were not important in promoting dispersal. Dobson (1979) also rejected the hypothesis that dispersal of juvenile male California ground squirrels *Spermophilus beecheyi* was influenced by the presence of adult male competitors since, after removal of adult males, the proportion of juvenile males dispersing remained the same as that before removal.

In contrast, Festa-Bianchet and King (1984) could not reject the possibility that aggression from adult males promoted dispersal of yearling male and female Columbian ground squirrels; yet Hackett (1987) found no evidence to support the possibility that adult male agonism influenced yearling dispersal of *S. columbianus*. He reported, instead, that dispersal of yearling Columbian ground squirrels was related to agonism on the natal home range from closely related kin. Specifically, aggression from reproductively active mothers forced dispersal of yearling offspring from the maternal home range (natal site) while siblings competed to retain proximity to the natal site -- sisters usually outcompeted brothers and usually only the most dominant sister could remain philopatric.

I studied the behaviour and dispersal of Columbian ground squirrels in areas where the habitat and social structure differed from that studied by Festa-Bianchet and King (1984) and Hackett (1987) (Chapter 3). Hackett reported that yearling siblings lived on the natal home range along with their mother (when present). In my study yearling males and females usually lived away from the mother and inhabited, instead, a "common" home range with other yearlings (including siblings) and usually one to several adult males (Chapter 3). The spatial relations of yearlings and adults in Festa-Bianchet and King's (1984) study appeared to be intermediate between that noted by Hackett (1987) and me (Chapter 3). In their study yearlings spent a proportion of each day in their natal area but also congregated onto areas away from adult females and their natal areas, where they foraged and played.

One would predict that interactions with close spatial associates, whether closely related or not, would be more important in initiating dispersal than would interactions with spatially isolated kin (ie. mothers in this study). Therefore, I tested whether the presence or absence of the mother and/or littermate sisters affected the likelihood of yearling dispersal (as reported by Hackett 1987) by experimentally removing mothers and/or littermate sisters of individual yearlings. As well, I tested whether the ratio of adult male competitors to adult females affected the likelihood that yearlings would disperse by experimentally altering the sex ratio in three colonies of Columbian ground squirrels in southwestern Alberta. The results of these manipulations are discussed in the light of the conspecific aggression hypothesis and hypotheses regarding the evolution of dispersal (Holekamp 1984).

Methods

The behaviour and dispersal of individual yearling Columbian ground squirrels was studied at three sites (NFW, NFE, and RG - see Chapter 2 for description) over the years 1984-1986. During this time kinship and demographic data were collected. Additional kinship and demographic data were available from colony DC for the years 1979-1985 (see Festa-Bianchet 1982, Festa-Bianchet and King 1984, and Chapter 2 for descriptions). Individuals in all four colonies were identifiable through serially numbered eartags (one in each ear) and unique body dye marks (Festa-Bianchet and King 1984 and Chapter 2). All members of each population were marked and followed over time. Details of trapping and observations are given in Festa-Bianchet 1982, Festa-Bianchet and King 1984, and Chapters 2 and 3.

Kinship was determined matrilineally. A juvenile's mother was assumed to be that female that actively defended the nest burrow from which the juvenile first emerged (Festa-Bianchet 1982, King 1984, Waterman 1986, Hackett 1987). A juvenile's littermate siblings were considered to be those juveniles that emerged (along with the animal in question) from the same natal burrow.

Dispersal status of individual yearlings was determined as outlined in Chapters 2 and 3. "Nondispersers" were yearlings that remained on or near their natal site and retained the same suite of neighbouring conspecifics. "Dispersers" were yearlings that permanently departed from both the natal site and their former neighbours (see Chapter 3 for further details and discussion). "Intracolony dispersal" refers to dispersal movements that occurred within the confines of the natal colony whereas "intercolony dispersal" refers to movements between colonies (see Chapter 2 for a definition of "colony"). Confirmed intercolony movements were classed as "known intercolony dispersal" whereas disappearance of individual yearlings from the natal colony during the "dispersal period" were classed as "presumed intercolony dispersal"; see Chapter 2 for further discussion. For yearlings living at colony DC, dispersal status could only be defined in terms of whether or not the yearling remained within or departed from the natal colony; eg. "colony philopatry" versus presumed or known "intercolony dispersal" (Chapter 2).

In 1986 a series of removals (and a few transfers) were undertaken at NFW, NFE, and RG in order to test the effects of adult sex ratio and the presence/absence of female kin on the tendency of individual yearlings to disperse. At NFE 12 of 15 and at RG 5 of 7 adult males were removed (Appendix 8). At NFW no adult males were removed but two were successfully transferred into the colony (details of transfer methods are given in Appendix 14). The goal was to produce two colonies (NFE and RG) with a low adult male to adult female ratio relative to ratios observed in unmanipulated colonies (eg. ≤0.25 males per adult female) and one colony (NFW) with a high adult male/female ratio (eg. ≥0.75 males per female - Table 6.1). The cumulative ratio of adult males to females in unmanipulated C1 and C2 colonies was 0.60 (294 males/497 females, n = 48 colony years). After male removals and transfers the adult sex ratios (males/females) were NFW (0.88), NFE (0.12), and RG (0.22)

Within each of the three colonies where sex ratio was manipulated a number of yearlings (21 males and 6 females) had their mother removed to test the effect of the absence of their mother on yearling dispersal tendency; the number of adult females removed were NFW (four), NFE (five), and RG (three), respectively (Appendix 8). Two of the four adult females removed from NFW were transferred successfully into NFE. Transfers were undertaken in an attempt to keep post-manipulation densities as close to original densities as possible. Spring population size after removal and transfer declined by the following percentages NFW (2.1%), NFE (21.1%), and RG (17.9%) (Appendix 10). Even after these manipulations, the spring population in 1986 was the same or larger than that recorded in the spring populations of 1984 and 1985 at each of the three colonies (Appendix 8).

The intent of these manipulations was to determine how dispersal of yearlings (mostly males) was affected by adult sex ratio and presence or absence of female kin (mothers and sisters Table 6.1). The experimental design provided four categories of yearling males: those with both their mother and sister(s) present, those with only a mother present, those with only a sister(s) present, and those without either a mother or sister(s). These 4 kinship categories occurred in the three populations with different adult sex ratios (Table 6.1). For additional analyses of the correlates of kinship and dispersal (disregarding colony sex ratio), data from three colonies (NFW, NFE, and RG) were combined for the years 1985-1986. In total 40 male yearlings had both mother and at least one littermate sister present, 26 had only the mother present, 18 had only the littermate sister(s) present, while 14 had neither mother nor littermate sister(s) present.

In 1986, the majority (69%) of yearling females bred. Since breeding affects the likelihood of dispersal (no yearling females that bred dispersed or disappeared during the dispersal period - Appendix 15), most yearling females had to be excluded from analyses of

Table 6.1 Number of yearling male Columbian ground squirrels in four categories of kin and two categories of adult sex ratio at colonies NFW, NFE, and RG in 1986.

	Adult sex ratio M/F High NFW 1986 = 0.88	Adult sex ratio M/F Low NFE 1986 = 0.12 RG 1986 = 0.22
Mother and littermate sister(s) present	12	14
Only mother present	5	5
Only littermate sister(s) present	5	8
Mother and littermate sister(s) absent	5	6

the 1986 experimental manipulation which reduced sample sizes below that required for statistical analysis. Thus most data on demography and kinship reported for yearling females comes from 1984 and 1985 before any experimental removals or transfers were undertaken.

Statistical procedures follow those outlined in Sokal and Rohlf (1981) and Zar (1981). Differences were considered significant when $P \leq 0.05$.

Results

The results of the experiment involving manipulation of numbers of adult male and female kin are summarized in Table 6.2. Only the results for yearling males are presented since most yearling females bred in 1986 (Appendix 8). Yearling males with female kin (mother and/or littermate sisters) were not significantly more likely to disperse either from the "natal site" or from the natal colony than were yearling males without female kin (Table 6.2). Six of the seven yearling males that remained in their natal sites (nondispersers) were in the two colonies (NFE and RG) that had very low ratios of adult males to females; only one male nondisperser was recorded at NFW where the adult sex ratio was much less female biased (Table 6.2). Among males that remained in their natal colony (nondispersers and intracolony dispersers), significantly more remained in the two colonies with a large female bias in the sex ratio than from the colony (NFW) with a less biased sex ratio (Table 6.2).

In the two colonies (NFW and RG) where the adult sex ratio was altered beyond the range previously recorded, the proportion of male intercolony dispersers also changed significantly(Table 6.3). More males dispersed when the adult sex ratio was less female-biased and vice-versa (Table 6.3). At NFE the adult sex ratio in 1986 was as low as previously recorded but the intercolony dispersal rate was at about the maximum level recorded before 1986(Table 6.3). A plot of the rate of colonial philopatry versus the adult male-adult female sex ratio for yearling males that resided in C1 colonies (see Chapter 2 for description) revealed that as the adult sex-ratio became less female biased the proportion of yearling males remaining in the natal colony dropped significantly (Fig. 6.1a). For yearling females the adult

Table 6.2 Summary of the dispersal status of yearling male Columbian ground squirrels that resided at NFW, NFE, and RG in 1986 relative to experimentally manipulated parameters of kinship and demography (see text for further details).

	Number of nondispersing yearling males/total number of yearling males present prior to dispersal (%)				Number of yearling males that remained in the natal colony (nondispersers plus intra-dispersers)/total number of yearling males present prior to dispersal (%)			
	Ratio adult males/adult females				Ratio adult males/adult females			
Female kin	High >0.75	Low <0.25	Difference[1]	Total	High >0.75	Low <0.25	Difference[1]	Total
Present (mother and/or littermate sisters)	1/22 (4.5)	5/27 (18.5)	$\underline{P} > 0.05$	6/49 (12.2)	3/22 (13.6)	12/27 (44.4)	$\underline{P} \leq 0.001$	15/49 (30.6)
Absent (no mother or littermate sisters)	0/5 (0)	1/6 (16.7)	$\underline{P} > 0.05$	1/11 (9.1)	1/5 (20.0)	2/6 (33.3)	$\underline{P} > 0.05$	3/11 (27.3)
Difference[2]	$\underline{P} > 0.05$	$\underline{P} > 0.05$		$\underline{P} > 0.05$	$\underline{P} > 0.05$	$\underline{P} > 0.05$		$\underline{P} > 0.05$
Total	1/27 (4.0)	6/33 (18.2)	$\underline{P} > 0.05$	7/60 (11.7)	4/27 (14.8)	14/33 (42.4)	$\underline{P} \leq 0.05$	18/60 (0.30)

[1] Difference between sex ratio categories based on Chi^2 test

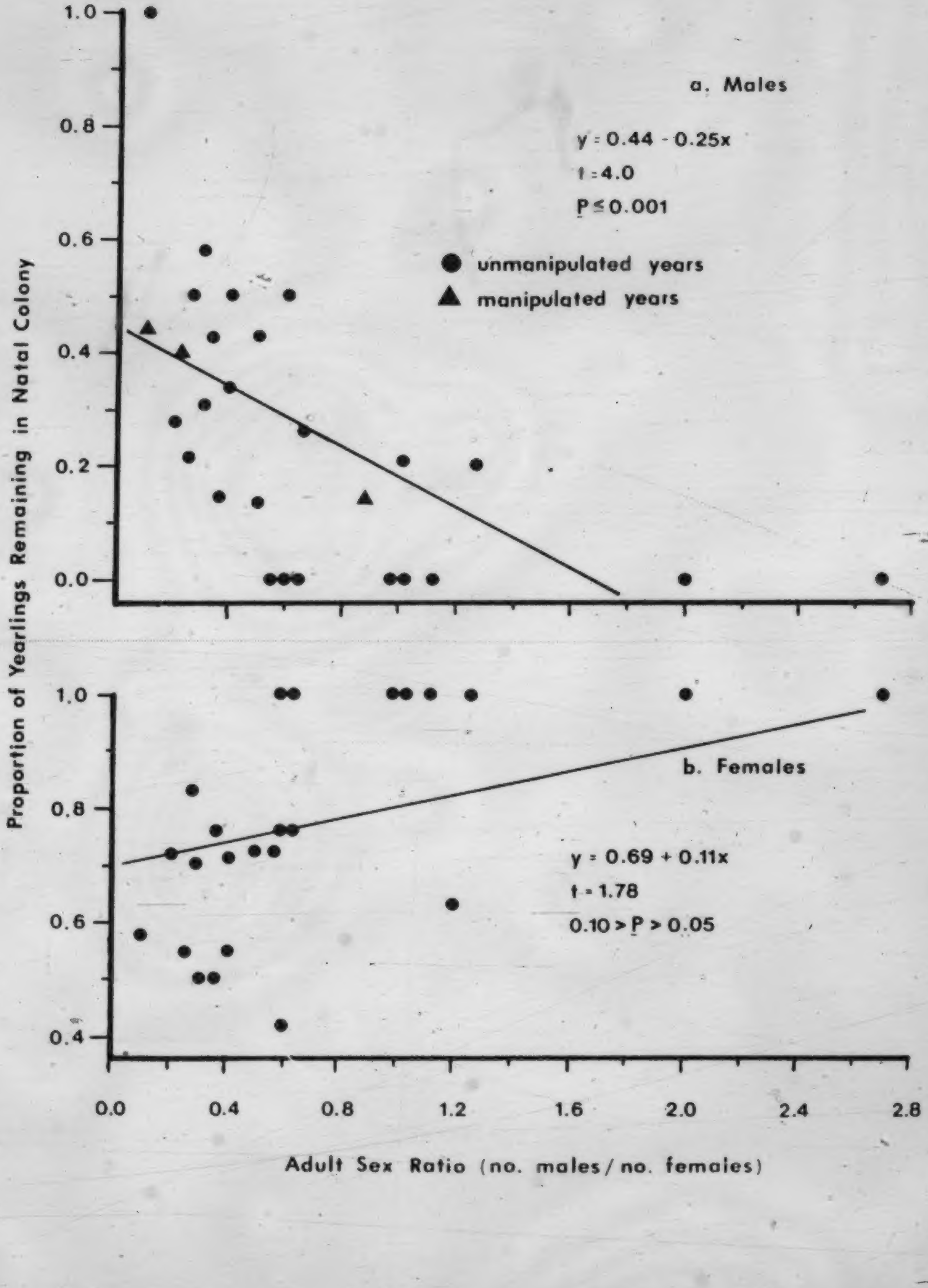
[2] Difference between kinship categories based on Chi^2 test

Table 6.3 Adult sex ratios and proportions of yearling male Columbian ground squirrels known or presumed to have dispersed from three colonies (NFW, NFE, and RG) before and after sex-ratio manipulation.

Colony	Years studied	Adult sex ratio male/female		Proportion of yearling males known or presumed to have dispersed		Difference[1]
		Before manipulation x (range)	After manipulation (1986)	Before manipulation x (range)	After manipulation (1986)	
NFW	1983-1986	0.32 (0.25-0.41)	0.88	0.63 (0.43-0.79)	0.93	$\underline{P} \leq 0.001$
NFE	1982-1986	0.34 (0.11-0.60)	0.11	0.40 (0.00-0.59)	0.56	$\underline{P} > 0.05$
RG	1979-1986	1.23 (0.6-2.7)	0.22	0.92 (0.8-1.0)	0.60	$\underline{P} \leq 0.01$

[1] Based on Chi^2 test

Fig. 6.1. The relationship between adult sex ratio and degree of colony philopatry among yearling male and female Columbian ground squirrels. Data are from colonies NFW, NFE, RG, DC, AA, and AB (n = 28 colony-years).


a. Males
y = 0.44 - 0.25x
t = 4.0
P ≤ 0.001
● unmanipulated years
▲ manipulated years
b. Females
y = 0.69 + 0.11x
t = 1.78
0.10 > P > 0.05
Proportion of Yearlings Remaining in Natal Colony
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.4
0.8
1.2
1.6
2.0
2.4
2.8
Adult Sex Ratio (no. males / no. females)

sex ratio was not significantly correlated with the proportion of females remaining in their natal colony.(Fig. 6.1b)

There did not appear to be any interactive effect between the presence or absence of female kin and the adult male to female sex ratio on the propensity of yearling males to disperse either from the natal site or the natal colony (Table 6.2). For example, yearling males without female kin that lived in colonies with a highly female-biased sex ratio (NFE and RG) were no more likely to remain on the natal site or in the natal colony than were those males with close female kin that lived at NFW where the adult sex ratio was less female biased (natal site; $X^2 = 1.044$; $0.50>P>0.25$ - natal colony; $X^2 = 1.247$; $0.50>P>0.25$).

Individuals from the 1985 and 1986 yearling cohort fell into one of four groups: those with both their mother and sister(s) present, those with only their mother present, those with only sister(s) present, and those with neither mother nor sister(s) present. Within each of these kinship categories the numbers of dispersers and nondispersers were compared. Among yearling males, there were no significant differences between proportions of nondispersers and dispersers in any of the four kinship categories (Table 6.4). In particular, where differences had been postulated (eg. between males with mother and sister(s) present versus males with the mother and sister(s) absent), no differences were recorded (Table 6.4). Moreover, there was no apparent relationship between the presence or absence of the mother and the dispersal status of yearling males (Table 6.4). Yearling male nondispersers had an average of 1.1 female kin present during their tenure as yearlings compared with dispersers (intra- and intercolony) with 1.5 female kin present, a nonsignificant difference ($X^2 = 1.12$, $0.25>P>0.10$).

Among yearling females, significantly more individuals with the mother and sister(s) present were likely to remain on or near the natal site than to disperse from it (Table 6.5) as is also suggested from Fig. 6.2b. Conversely, those females without mothers and sister(s) were significantly more likely to emigrate from the natal site than to remain (Table 6.5). Moreover, yearling females with a mother present were more likely to remain on the natal site

Table 6.4 Proportion of dispersing (86) (intra- and intercolony) and nondispersing (12) yearling male Columbian ground squirrels that had their mother and/or littermate sister(s) present or absent from the natal colonies NFW, NFE, and RG during their tenure in these colonies as yearlings.

	Mother present		Difference[1]	Mother absent		Difference[1]
	Nondispersers	Dispersers		Nondispersers	Dispersers	
Sister(s) present	$^{3}/12$ (0.25)	$^{37}/86$ (0.43)	$P > 0.05$	$^{3}/12$ (0.25)	$^{15}/86$ (0.17)	$P > 0.05$
Sister(s) absent	$^{4}/12$ (0.33)	$^{22}/86$ (0.26)	$P > 0.05$	$^{2}/12$ (0.17)	$^{12}/86$ (0.14)	$P > 0.05$
Total	$^{7}/12$ (0.58)	$^{59}/86$ (0.69)	$P > 0.05$	$^{5}/12$ (0.42)	$^{27}/86$ (0.31)	$P > 0.05$

[1] Based on Fisher's Exact Test

Table 6.5 Proportion of dispersing (intra- and intercolony dispersers) (16) and nondispersing (23) female Columbian ground squirrels that had their mother and/or littermate sisters present or absent from the natal colonies NFW, NFE, and RG during their tenure in these colonies as yearlings.

	Mother Present		Difference[1]	Mother Absent		Difference[1]
	Nondispersers	Dispersers		Nondispersers	Dispersers	
Sister(s) present	13/23 (0.57)	2/16 (0.13)	$\underline{P} \le 0.01$	3/23 (0.13)	3/16 (0.19)	$\underline{P} > 0.05$
Sister(s) absent	6/23 (0.26)	6/16 (0.38)	$\underline{P} > 0.05$	1/23 (0.04)	5/16 (0.38)	$\underline{P} \le 0.05$
Total	19/23 (0.83)	8/16 (0.50)	$\underline{P} \le 0.05$	4/23 (0.17)	8/16 (0.50)	$\underline{P} \le 0.05$

[1] Based on Fisher's Exact Test

than were those females without a mother. In fact, nondispersing females had twice as many close female kin present as did females that were known or presumed intra- and intercolony dispersers (nondispersers, x = 1.65 female kin per female; dispersers, x = 0.88 female kin per female), a difference that was significant ($X^2 = 4.57$, $0.05>P>0.025$).

With regard to male kin, in this case littermate brothers, neither yearling male nor yearling female dispersal status was correlated with the presence or absence of brothers (Table 6.6). As well, neither male nor female nondispersers differed significantly from dispersers in the average number of brothers that each group had although male nondispersers tended to have fewer brothers than did male dispersers (nondispersers = 0.42 brothers; male dispersers = 0.83 brothers · $X^2 = 2.265$; $0.25>P>0.10$). Female nondispersers had on average 1.0 brothers present whereas female dispersers had 1.2 ($X^2 = 0.0579$; $0.90>P>0.75$). In total only 6 yearlings (all male) had no close kin of either sex present (mother, littermate brothers, and littermate sisters absent) during the yearling's tenure in the natal colony. Four of these males eventually disappeared during the dispersal period whereas the other two males remained near their natal area. Thus, it appears that the complete absence of close kin (the mother, and littermate siblings of either sex) has little affect on the likelihood of dispersal in yearling males.

Although the likelihood of yearling male dispersal or disappearance from the natal site was not correlated with any measures of known kinship (Table 6.2 and 6.4), dispersal and disappearance from the natal colony did appear to vary with kinship. For example, Table 6.7 shows the proportion of yearling males that remained in the natal colony and those that presumably dispersed from it as a function of the presence or absence of the mother. At NFE and RG there were no significant differences between the proportion of males that remained within the confines of the natal colony versus those that presumably dispersed from the natal colony relative to the presence of their mothers. On the other hand, at NFW and DC fewer individuals remained within their natal colony when their mothers were present than when absent. The pooled data indicate the same relationship; greater dispersal of those males that

Table 6.6 Proportion of dispersing and nondispersing male and female Columbian ground squirrels that had littermate brothers present during their tenure as yearlings at colonies NFW, NFE, and RG. Sample sizes in parentheses.

	Nondispersers	Dispersers	Difference[1]
Male	0.42 (12)	0.63 (86)	$P > 0.05$
Female	0.74 (23)	0.81 (16)	$P > 0.05$

[1] Based on Chi^2 test

Table 6.7 Comparison of the percent of yearling male Columbian ground squirrels that had no mother present relative to colony dispersal status.

Colony-Year	% of philopatric males without mothers (n)	% of intercolony dispersers without mothers (n)	Difference[1]
RG-1985/86	50.0 (6)	64.7 (17)	$\underline{P} > 0.05$
NFE-1985/86	73.3 (15)	80.0 (20)	$\underline{P} > 0.05$
NFW-1985/86	33.3 (9)	74.2 (31)	$\underline{P} < 0.05$
DC-1980/86	52.6 (19)	92.6 (54)	$\underline{P} < 0.001$
Pooled Data	55.0 (49)	82.0 (122)	$\underline{P} < 0.001$

[1] Based on Chi^2

had their mother present. Similarily, the total proportion of yearling males having no close female kin (neither mother nor littermate sisters) that remained in their natal colony was significantly higher than for those males that presumably dispersed from the natal colony (Table 6.8).

Including all three colonies (NFW, NFE, and RG) over 2 years (1985 and 1986), I recorded only one yearling female making an intracolony dispersal movement. Thus for yearling females comparisons between colony philopatry and intercolony dispersal are essentially equivalent to the comparison made earlier between nondispersers and dispersers. Yearling females that remained in their natal colony were characterized by having a greater proportion and a greater absolute number of close female kin present in the natal colony than were those females that dispersed or presumably dispersed from the natal colony (Table 6.3).

In summary, yearling male dispersal was correlated more with adult sex ratio (adult males to adult females) than with known categories of kinship. Greater rates of dispersal and lower levels of colony philopatry occurred when the adult sex ratio was less female biased; in other words, when there were a relatively fewer adult males. Male dispersal was not correlated with the presence or absence of various categories of female kin or with the presence or absence of littermate brothers. As well, the absolute numbers of close male and female kin did not differ significantly between male nondispersers and dispersers. On the other hand, colony philopatry by yearling males was correlated with the number of female kin present in two of the four colonies studied. Specifically, individual yearling males at colonies NFW and DC that had their mother or mother and sister(s) present were significantly more likely to disperse or disappear from the natal colony than were those individual males that had no mother or no mother and littermate sister(s). Presumed dispersal of yearling females from both the natal site and the natal colony was significantly correlated with the presence of female kin. Yearling females with no mother or no mother and sister(s) were signficantly more likely to disperse or disappear from the natal site or natal colony than were those females that had either the mother present or both the mother and sister(s) present. This was reflected to a degree in the

Table 6.8 Comparison of the percent of yearling male Columbian ground squirrels that had neither mother nor littermate sisters present relative to colony dispersal status.

Colony-Year	% of philopatric males without female kin (n)	% of intercolony dispersers without female kin (n)	Difference[1]
RG-1985/86	0.0 (6)	0.0 (17)	$\underline{P} > 0.05$
NFE-1985/86	13.3 (15)	20.0 (20)	$\underline{P} > 0.05$
NFW-1985/86	55.6 (9)	9.7 (31)	$\underline{P} < 0.05$
DC-1980/86	36.8 (19)	5.5 (54)	$\underline{P} < 0.01$
Pooled Data	28.6 (49)	8.2 (122)	$\underline{P} < 0.01$

[1] Based on Chi^2 test

trend between adult sex ratio and female philopatry.

Discussion

The removal experiment involving adult male and female kin

The results of the removal experiment involving adult male and female kin suggested that yearling males were less likely to disperse from their natal site and/or their natal colony when adult male density (relative to adult female density) was low. The presence or absence of close female kin (mothers and sisters) seemed not to influence yearling male dispersal nor was there an apparent synergistic effect between male density and the presence of female kin on yearling male dispersal behaviour (Table 6.2 and 6.4).

The possibility that the results of these experiments were an artifact of the removals, and that the reduced number of adult males at NFE and RG was not the reason why yearling males remained but rather the presence of unoccupied vacancies in the colony which produced increased rates of philopatry, does not seem to have been the case.

In total 32 vacancies were made available at NFW, NFE, and RG through adult removals (12 females and 17 males) and the overwinter disappearance of three additional adult females. Nine of 18 yearling males that remained within the natal colony in 1986 came to settle partially or completely on nine vacancies created by removal of previous residents (eight males and one female). Among the other nine males, five insinuated themselves onto areas occupied by other squirrels while four established residency on vacancies created by a change in the habitat. Prior to emergence of ground squirrels in 1986, the forested areas surrounding colony RG were removed by Alberta Forestry and the felled trees were placed into numerous log piles. Yearling males often took cover under these log piles during their excursionary movements, four of them eventually dug burrows thereunder, and settled away from the main colony area. Of the 12 nonbreeding yearling females that remained in their natal colony, only three (25%) filled vacancies created by the removals and disappearances.

All the others settled on or near their natal home areas (for further details see Chapter 3). Thus, it appeared that some of the yearlings that remained may have done so because a vacancy was available. Nevertheless, not all yearlings settled in the created vacancies, 14 of 30 (47%) established in areas where no vacancy was created by either removals or habitat manipulation.

Additional evidence suggests that it was low numbers of adult males that resulted in high rates of site and colony philopatry of yearling males rather than the availability of vacancies *per se*. In the three main study sites and at other Ci colonies, rates of colony philopatry of yearling males were inversely correlated with adult sex ratio (Fig. 6.1). Natural fluctuations in the adult sex ratio from year to year were due primarily to differential recruitment rather than differential mortality of the sexes. In other words, adult sex ratio became more female-biased in years when yearling female recruitment into the population the previous season was high, for example in years when yearling females bred. Conversely the population became more male-biased subsequent to greater yearling male recruitment through immigration and/or philopatry. Thus changes in the sex ratio from year to year, resulting from differential recruitment and not mortality, meant that few vacancies were available each spring. When vacancies were available through overwinter disappearance, adult females were most likely to fill them (person. obs.). Thus fluctuating sex ratios did not result in increased vacancies; in fact, the extent of recruitment of one sex, necessary to alter sex ratios, usually meant that the size of population had to rise (eg. see Appendix 8) and thus vacancies were probably fewer. Despite this more males remained in their natal colony when the adult sex ratio became more female-biased.

Why should yearling males be affected by the adult sex ratio? Both adult males and adult females are aggressive towards yearlings. Adult female aggression is related to the reproductive cycle (Festa-Bianchet and King 1984, Hackett 1987, Chapter 4). Those females that breed and have litters become aggressive and this aggression is not discriminatory; all age and sex categories of conspecifics are involved (Chapter 4). Adult males on the other hand show significant differences in their agonistic tendencies. Not only are there great individual differences among adult males, 2-year-old males as a group behave much more aggressively towards yearling males than do older adult males. Two-year-old males are apparently forced by older more dominant males (*cf* Murie and Harris 1978) and by adult females to occupy "communal" areas with the less agonistic yearling cohort (Chapters 3 and 4). Within the communal area, 2-year-old males consistently "bully" the yearlings (especially males) and dispersal of yearling males from communal areas occupied by 2-year-old males tends to be greater than from communal areas without these males or from communal areas with only older neighbouring males (Chapter 4). Thus lower rates of site and colony philopatry of yearling males occurred when there were more 2-year-old males in the colony which was in turn when the adult sex ratio of the colony was more male-biased. Hence the sex ratio *per se* may not be important but rather the age structure of the male cohort; the more 2-year-old males present, the more likely yearling males were to disperse.

Yearling female dispersal, on the other hand, was apparently less influenced by fluctuations in the adult sex ratio (Fig. 6.3). This is surprising since neither adult males nor females treated yearling females differently from yearling males (Chapter 4). Nevertheless, yearling females seemed much less affected by high rates or frequencies of agonism than did yearling males. Yearling females lived closer to their mother than did yearling males even during the period when mothers were highly aggressive (Chapters 3 and 4). Yearling males appeared to avoid both the mother, other adult females, and adult males, more so than did yearling females, and aggression from 2-year-old males seemed more intense (though not more frequent) toward yearling males than yearling females (Chapter 4).

Whatever the reason, yearling male dispersal and philopatry were correlated with adult sex ratio, the former being higher when the sex ratio was more male-biased and contained proportionally more 2-year-old males. Yearling female dispersal, on the other hand was less correlated with the adult sex ratio but more with the presence or absence of close female kin (especially the mother - Table 6.5).

The maternal aggression/yearling competition hypothesis

Hackett (1987) concluded that dispersal of yearling Columbian ground squirrels off the natal home range was proximally caused by maternal aggression and inter-sibling competition. Reproductively active mothers drove their yearling offspring off the natal home range in defense of their new litters; yearling siblings then competed with each other to retain proximity to the natal home range. Yearling sisters generally outcompeted their male siblings and among sisters usually only the dominant sister remained; all others dispersed. Hackett believed that yearling males dispersed unless they encountered little aggression from close female kin (ie. when they had no sisters alive and the mother was dead or not pregnant). Based on Hackett's findings one would predict that female dispersal should occur only from multi-female litters and that males should remain on the natal home range only when few or no close female kin were present or when their mothers were not reproductively active.

In this study only 5 of 16 female dispersers were the products of multi-female litters (Table 6.5); the remaining 11 all lacked yearling sisters. One half (50%) of all female dispersers did not have their mother present during their tenure as yearlings compared to only 17% of nondispersers (Table 6.5). The greatest number of female dispersers was expected to be among those females that had both their mother and sisters present; in this category only 2 of 15 females dispersed, the lowest dispersal rate among all categories recorded (Table 6.5). Thus, in general, those yearling females with the fewest close female kin dispersed while those with the greatest number of kin remained on or near the natal site - completely contrary to the predictions of Hackett (1987).

Among yearling males there was no apparent correlation between the presence or absence of close female kin and tendency to disperse. Of the 14 yearling males that had no mother or sisters present (the group predicted most likely not to disperse) 12 eventually dispersed or disappeared (Table 6.5). Thus the predictions of Hackett's hypothesis were also violated for yearling males.

The kinship predictions of Hackett's maternal aggression and yearling competition hypothesis were not upheld in my study. In fact, my findings are almost completely opposite to those of Hackett's. The answer to this apparent contradiction may not lie in the validity of Hackett's hypothesis and predictions but rather whether they are applicable to the situation in the populations that I studied. The spatial relations among yearlings and adults on my three study areas were vastly different from those of Hackett's sites (Chapter 3). All yearlings on Hackett's study site emerged from and lived within their mothers' home range (their natal area) during the first several 10-day periods of the active season. Under such a situation it is not surprising that dispersal was related to conditions on the natal site since family members (mother and her yearling offspring) all resided on one small area. In my study, yearlings did not emerge from nor live on the natal home area. All non-breeding yearlings resided with other yearlings in communal areas away from their natal areas (Chapter 3). Thus in cases such as this it is not surprising to find that conditions on the natal site had little influence on the dispersal tendency of yearlings. Instead it appeared that conditions within the communal area were important determinants of future dispersal status - at least for yearling males.

Among males the largest (heaviest), apparently more dominant individuals tended to remain on or near the communal area and/or natal home range whereas lighter, more subordinate individuals tended to disperse (Chapters 4 and 5). Among dispersers intracolony dispersers tended to be heavier and more dominant than intercolony dispersers (Chapters 4 and 5). Thus heavy dominant males tended to remain in their natal colony while lighter more subordinate males tended to disperse from it. Hackett (1987) found no relationship between dominance and dispersal status for yearling males probably because males on his areas resided on or near their natal area and hence associated mainly with their siblings. Thus male yearlings had less opportunity to interact with and establish dominance relationships with any other yearling male except their littermates. Generally male yearlings with female kin (mother and/or sisters) dispersed and thus dominant brothers had little opportunity to influence the dispersal of their subordinate brothers since both were "forced" to leave because of agonism from the mother and littermate sisters.

In my study, although yearling females usually lived away from their natal home range on communal areas (Chapter3), interactions with conspecifics on the communal area did not appear to influence dispersal as it did for yearling males (Chapter 4); instead dispersal of yearling females was correlated with kinship. Most females with mothers present returned to the natal site after juvenile emergence when maternal aggression had subsided (Chapter 4). These females eventually established on or adjacent to the natal area independent of the number of littermate sisters. Those females with no mother and/or sisters present were usually unable to return to the natal area because whenever a vacancy was created by removal or death of an adult female, that vacancy was quickly filled by another adult female or by several adult females that had each expanded their home ranges to occupy portions of the vacancy. For example 12 of 15 vacancies created by removal or disappearance of adult females were filled by other possibly "unrelated" adult females (in most cases exact relationships of adult females were unknown). Yearling females usually could not become established in their former natal area if "unrelated" (nonmother) adult females had taken over the vacancy. Therefore, usually only females with close female kin could re-establish themselves on their former natal area. Apparently mothers permitted their yearling daughters to return to the natal area after juvenile emergence whereas offspring of other adult females were not allowed to settle. Harris and Murie (1984) reported that yearling daughters of *S. columbianus* apparently inherited their mothers former nest site in some cases. In this study there was also some evidence of mothers relinquishing the maternal home range to their reproductively active yearling daughters (Appendix 12). In light of these findings it is understandable why only those yearling females with female kin were able to stay in these relatively high density colonies (Appendix 9).

Although male dispersal was not related to kinship at any of the colonies studied (ie. nondispersers and dispersers did not differ significantly in kinship parameters), males that remained at colonies NFW and DC (nondispersers and intracolony dispersers) had significantly fewer female kin than did known or presumed intercolony dispersers; trends that were similar but not significant at NFE and RG; Tables 6.7 and 6.8). One possible explanation for these differences between colonies may relate to differences in spatial organization. At colony DC, yearlings did not live away from their natal home range in communal areas as I found for yearlings in my study. Instead, yearlings appeared to divide their time between the maternal home range and other areas away from adult females where they gathered to play (Festa-Bianchet and King 1984, King person. comm.). That yearling males at DC were apparently still associated in space (to a degree) with their mothers (and presumably their sisters) may explain why dispersal from that colony was related to the presence of female kin. At NFW, NFE, and RG males generally lived away from the maternal home range (Chapter 3) and dispersal did not seem to be correlated with kinship (Tables 6.2 and 6.5) except at NFW where males without female kin were more likely to remain than males with female kin.

Another possible explanation for the relationship observed between colony philopatry and kinship for yearling males at NFW and DC may have been related to differences in dominance status. Among yearling males in this study dominance status was correlated with weight (Chapters 4 and 5); larger males appeared to dominate smaller males (Chapter 4). Larger more dominant males tended to be more philopatric than smaller males (within limits). Since nondispersing males tended to have fewer brothers and sisters than dispersers, they usually were the products of smaller litters. Individuals from small litters may begin life with a weight advantage and have more resources available on the natal home range as juveniles relative to individuals from larger litters. If this weight advantage carries over to yearlings then individuals from smaller litters would tend to be larger animals. Larger males appear to be more dominant and the most dominant males tend to be philopatric (Chapter 4). Thus the relationship between colony philopatry and kinship for yearling males in this study may be an indirect relationship. Males with fewer female kin may remain in their natal colony not necessarily because of the absence of these kin but because fewer kin may mean less resources to share, more growth, and greater dominance status - dominant individuals remained possibly because they could obtain and defend vacancies from other less dominant yearlings (Chapter 4).

Evolutionary perspectives

In this study it appeared that spatial associates were more important as proximal stimuli in prompting the dispersal of yearling males than were kin. It could be argued, however, that the mother by preventing the return of her yearling male offspring to the maternal site after spring emergence ultimately forced her sons to live in situations that later would prompt their dispersal. Nevertheless, the evidence suggests that it was interactions while on the communal area that were the proximal stimuli determining the dispersal status of individual males and not the initial bout of agonism from the mother that later caused dispersal. For example, 12 of the 14 yearling males with neither their mother nor their littermate sisters present were either known (3 males) or presumed (9 males) to have dispersed. In the light of these observations, I suggest that dispersal of yearling males in Hackett's study was simply a consequence of their spatial association with kin and not that "kinship" *per se* played any role in initiating dispersal.

A number of authors have postulated that natal dispersal in birds and mammals evolved as a mechanism to prevent consanguinous mating of close kin (Greenwood et al. 1978, Dobson 1979, Packer 1979, Pusey 1980, Dobson 1982, Cockburn et al. 1985, Holekamp 1986). In this study yearling males apparently did not disperse to avoid living near female kin; of the 12 yearling male nondispersers recorded in this study, 6 lived adjacent to or shared part of the same home range with either their littermate sisters or their mother during post dispersal periods as yearlings or as 2-year-olds. Furthermore, the absence of close female kin did not reduce the likelihood of dispersal from the natal site for yearling males (Tables 6.2 and 6.4). That yearling males often remained in the presence of and dispersed in the absence of female kin suggests that either dispersal was not primarily a means of avoiding inbreeding or that the proximate stimuli causing dispersal were relatively inefficient in preventing the spatio-temporal overlap of male and female kin.

On theoretical grounds, it is doubtful that dispersal could have evolved solely as a mechanism to prevent inbreeding because in order for populations to incur a "cost" to inbreeding they must first have outbred. A population having no dispersal should, in theory, be relatively inbred, the major "cost" of which is increased homozygosity which exposes deleterious recessive alleles (Packer 1979, Bateson 1983, Partridge 1983, Moore and Ali 1984, Ralls *et al.* 1986), accumulated only during outbreeding (Moore and Ali 1984). "Clearly if a species has never been outbred then deleterious recessives will not have had the opportunity to accumulate" (Moore and Ali 1984:96) and there would be no need for dispersal to evolve. It is possible, however, that, once sex-biased dispersal evolves (for whatever reason), outbreeding and greater heterozygosity will follow and as a consequence selection to avoid inbreeding may increase (Ralls *et al.* 1986). Thus, if inbreeding avoidance and dispersal are related (ie. as in *Anetchinus spp*, Cockburn *et al.* 1985), inbreeding avoidance is probably a secondary consequence of dispersal and dispersal likely evolved originally for other reasons. (Ralls *et al.* 1986).

I suggest that delayed dispersal in species like the Columbian ground squirrel may have evolved as a consequence of female reproductive strategies. All detected intruders (including close kin) are chased away from the vicinity of a female's nest burrow (Festa-Bianchet and Boag 1982, Hackett 1987, Chapter 4). This "territoriality" appears to function to protect young from intraspecific depredations and, as well, provides a resource base (food and a burrow system) which the young can use once they emerge (Festa-Bianchet and Boag 1982). Because of maternal aggression, yearlings are forced to live elsewhere, in the case of Hackett's study at the periphery of the natal home range, in the interstices among adult female territories or on communal home ranges away from adult females as in this study (Chapter 3). Maternal aggression is probably adaptive because it increases the reproductive success of the female in question (see discussion in Hackett 1987). Females that prevent the use of limited resources (eg. food, Dobson and Kjelgaard 1985a, b) on their "territory" by excluding intruders will probably guarantee better growth and subsequent survival of their juveniles (Murie and Boag 1984, Dobson and Murie 1987). As well, females may gain inclusive fitness benefits as a result of "dispersing" their yearling offspring (especially males) because the males will not ultimately be competing for mates with their relatives (brothers and/or father) which has been postulated to reduce the inclusive fitness among the related competitors (Smith 1979, Hackett 1987). As well, dispersal of males from the natal site would prevent sib-mating which from an inclusive fitness standpoint is less than ideal - a male would pass on more of "his" genes by mating with unrelated females and by having his sister mate with unrelated males than if siblings mated with each other (Chesser and Ryman 1986). Thus, dispersal, originally a mechanism to avoid aggresive interaction with mothers, may have ultimately resulted in increased inclusive fitness (Hackett 1987, Chapter 6) for both the mother and its siblings.

Contrary to males, female mammals should be selected to be relatively site tenacious (Greenwood 1980). Males in polygynous species (most mammals) invest little in offspring and have the most to gain from dispersal, while females invest heavily in offspring and gain the most from being sedentary (Clutton-Brock and Harvey 1976, Baker 1978, Packer 1979, Greenwood 1980). As well, females in polygynous species such as ground squirrels are not constrained by mate competition; very few males are necessary to inseminate a large number of females. For example, 3 males at colony NFE successfully inseminated at least 27 females in 1986. Thus females will not suffer the postulated decrease in inclusive fitness incurred by competing with relatives for mates (*sensu* Smith 1979). Female mammals are presumably more resource dependent than are males because of the costs associated with pregnancy and lactation, making it more advantageous for them to remain at the natal site where the resources necessary to raise young have already been proven adequate (Hackett 1987). Consequently, young female mammals should compete more fiercely than young males, and sisters should compete to remain on or near the natal site where adequate resources already have been proven (Pfeifer 1982, Hackett 1987). If resources were inadequate or "outcompeted" for by other sisters, then it would be in the "best interest" of the female yearling in question (and her female kin) to disperse in hopes of finding adequate resources uncontested elsewhere. Were adequate resources available on the natal area, inclusive fitness would be increased by having daughter(s) remain and share the natal site - the spatial and temporal overlap of female kin would provide a framework within which the evolution of nepotism could occur(Sherman 1981, Michener 1983).

In summary, theoretical considerations backed by empirical evidence suggest that male-biased natal dispersal in the Columbian ground squirrel probably did not evolve as a mechanism to avoid inbreeding. Dispersal of yearlings is explained most parsimoniously as a consequence of female reproductive strategies -- maternal aggression provides the initial stimulus resulting in movements away from the maternal home range but actual intercolony dispersal by males will depend on the yearling's social relations with spatial associates after leaving the natal site, whereas that of females will depend upon their association with kin relative to resource availability. Successful dispersal of yearling males probably results in enhanced reproductive potential by lessening competition for mates with male kin and increasing opportunities for mating with unrelated females. Female reproductive success is probably most enhanced, on average, by philopatry unless resources *in situ* are inadequate, when dispersal could be favoured.

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VII. Concluding Discussion

In this thesis I addressed two hypotheses dealing with the proximate causes of natal dispersal in the Columbian ground squirrel. No evidence was found to support the hypothesis that achievement of a critical weight threshold initiated dispersal of yearlings, although a minimum critical weight appeared necessary before an animal would undertake an intercolony dispersal movement. Dispersal at maximum weight presumably is a tactic to increase survival during and after immigration into a new colony.

I found no evidence to reject the hypothesis that conspecific aggression initiated dispersal of yearling *S. columbianus* . Indeed, spatial (Chapter 3), social (Chapter 4), and kinship and demographic (Chapter 6) variables were all related to dispersal behaviour. Each variable independently suggested that dispersal was socially induced apparently through conspecific aggression. For yearling females, dispersal appeared to depend on the presence or absence of female kin; philopatry was the norm for females with their mother present while dispersal was the norm for yearling females without their mother (Chapter 6). Apparently yearling female recruitement onto or adjacent to the natal home range was a result of the presence of kin, as yearling females without mothers did not settle on the natal site when an "unrelated" (non-mother) had taken it over. Hence most dispersal of yearling females was the result of their inability to re-settle on or near their natal home ranges, usually because of the absence of close female kin (mother and/or sisters). Some females with kin may have dispersed because their dominant sisters outcompeted them for limited space on the natal home range, but in most cases philopatry of yearling females was contingent on the presence of and on interactions with close female kin.

For yearling males (and females), initial return to the natal home range after emergence in the spring was apparently prevented by the aggressive behaviour of the reproductively active mother. Further movements of yearling males were the result of social influences within the yearling "communal" area (Chapters 3 and 4). Yearlings of both sexes lived on a common home area often with adult males but usually away fom the "territories" (*sensu* Festa-Bianchet and Boag 1982)of adult females (Chapter 3). Interactions with adult males, yearling males, and adjacent neighbouring adult females all apparently influenced the dispersal behaviour of yearling males whereas such interactions did not appear to influence female dispersal (Chapters 4 and 6). Nondispersing males usually were dominant to all other males in their communal area and as well were more likely to come from areas where there were fewer neighbouring adult males - especially 2-year-old males (Chapters 4 and 6). Thus, dispersal of yearling males subsequent to the initial movement away from the natal home range appeared to depend more upon interactions with close spatial associates (neighbours) than it did with female kin. Some males remained on or near the natal site in the presence of close female kin while others dispersed in the absence of such kin. Thus kinship seemed a less important influence on dispersal among males than among females.

The results of this study are consistent with those of Festa-Bianchet and King (1984) and Hackett (1987) who concluded that conspecific aggression initiated dispersal of yearling Columbian ground squirrels. The differences in the spatial and social relationships among adults in their studies and in mine were probably the result of differences in habitat structure (Chapter 3). As a result, the conspecifics responsible for influencing dispersal among yearlings often varied. For instance, in my study yearlings lived on communal areas with other yearlings and adult males and dispersal appeared to be influenced by interactions with these conspecifics, whereas in Hackett's study, yearling males lived on their natal home ranges with their mothers and sisters and these conspecifics apparently initiated the dispersal. Dispersal of yearling females away from the natal area in both Hackett's and my study appeared to be influenced by (interactions with female kin even when yearling females lived away from their natal sites (ie.)on communal areas in this study).

Females are probably selected to be philopatric because they invest disproportionately more in offspring than do males and thus are more tied to resources (Clutton-Brock and Harvey 1976, Packer 1979, Greenwood 1980, Pfeifer 1982, Hackett 1987, Chapters 4 and 6). Therefore, females might be expected to compete for "proven" resourc on the natal area

(Pfeifer 1982, Hackett 1987). Dominant sisters may force subordinates to disperse when resources on the natal area are limited (Pfeifer 1982, Hackett 1987,Chapter 6). In small isolated colonies where vacancies are limited, yearling females may be able to settle only if the mother is present and will relinquish part or all of the natal area to the yearling daughter (Chapter 6 and Appendix 12). Kin clustering on the natal area among females may be a female tactic that results in increased inclusive fitness (Michener 1983, Chapters 4 and 6).

As a result of tactics that increase female fitness (tenacity to the birth site and maternal aggression), males may be forced to disperse. Male dispersal may result in further inclusive fitness benefits for females as well as males (Chapters 4 and 6). For example, males will no longer compete for limited resources (eg. food) with kin, male kin will not compete for female mates, and males may increase the number of females with which they can mate and thereby increase the number of their and their female kin's genes (Chapters 4 and 6). Once established, dispersal may secondarily be reinforced by such mechanisms as inbreeding avoidance, competition for mates, and/or competition for resources; these mechanisms need not necessarily be the reason(s) why dispersal evolved but rather may only be secondary consequences of the behaviour once it became established (Chapters 4 and 6). The suggestion is that elucidation of the evolutionary causes of dispersal will more likely be determined if the immediate cause of dispersal is known (Holekamp 1983, Hackett 1987). Knowing the proximate stimuli causing dispersal is useful in determining what is reasonable to propose in terms of ultimate (evolutionary) causes (Hackett 1987).

The goal of future research remains to pinpoint the precise stimuli for dispersal in a wide-variety of species under a wide array of habitat and social conditions. As well, there remains the task of quantifying both the costs and benefits of dispersal and philopatry. Since costs and benefits probably vary between populations within a species (ie, populations in isolated versus continuous habitat), it will be important to determine costs and benefits in a number of populations before generalities can be made. For the Columbian ground squirrel this requires further work with populations in isolated meadows; specifically, information is lacking on in transit success of intercolony dispersers, and the fate of these dispersers as immigrants (eg. survival, fecundity, and lifetime reproductive fitness). Such information requires extensive long-term study, but is essential if our understanding of the causes and consequences of dispersal is to be complete. To the future, I look forward.

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VIII. Appendices 1 - 18

Appendix 1. The Classification of Montane Meadows into Continuous and Discontinous Habitat

Meadow areas with ground squirrel populations varied greatly in size in this study (0.34 to 72 ha; Table 2.1 Chapter 2). Although the 80% home range core areas of individual Columbian ground squirrels averaged only 0.05 to 0.10 ha (Appendix 7), squirrels that lived in small meadows (ie. 1-2 ha or less) apparently were ~~familiar with~~ the entire meadow as most individuals were sighted or captured at one time or another in nearly every section of their respective meadows. In small meadows individuals were almost always near their place of birth and former neighbours no matter where in the meadow they settled. In contrast, animals that lived in larger meadows (ie. 5 ha or greater) probably were not familiar with the entire meadow in which they lived and as well could settle in areas away from their natal site and former neighbours (*cf* Hackett 1987).

I defined habitat as continuous or discontinuous based on the size of the meadow. If the meadow was large enough to allow any individual in the population the ability to disperse and settle away from the natal site and former neighbours in at least two directions then I considered the habitat to be "continuous". Meadows too small to allow dispersal in two directions were considered "discontinuous". Individuals were considered to have dispersed if they settled two or more adult home range diameters (1 HRD = 40 m) from their natal site (Chapter 3). Based on these criteria (dispersal distance and area sufficient to disperse in at least two directions), a meadow would have to be a minimum of five adult home range diameters long and three wide (2.4 ha) or four by four HR (2.56 ha) to be "continous". Any meadow area smaller than 2.4 ha was considered discontinuous. In this study all meadows classified as discontinuous were smaller than 2.0 ha whereas all meadows classifed as continuous were larger than 3.0 ha in area (Table 2.1 Chapter 2). Although the criteria used to define continuous and discontinuous habitat were somewhat arbitrary, they were, nevertheless, based on an ecological scale that was meaningful to the animals studied.

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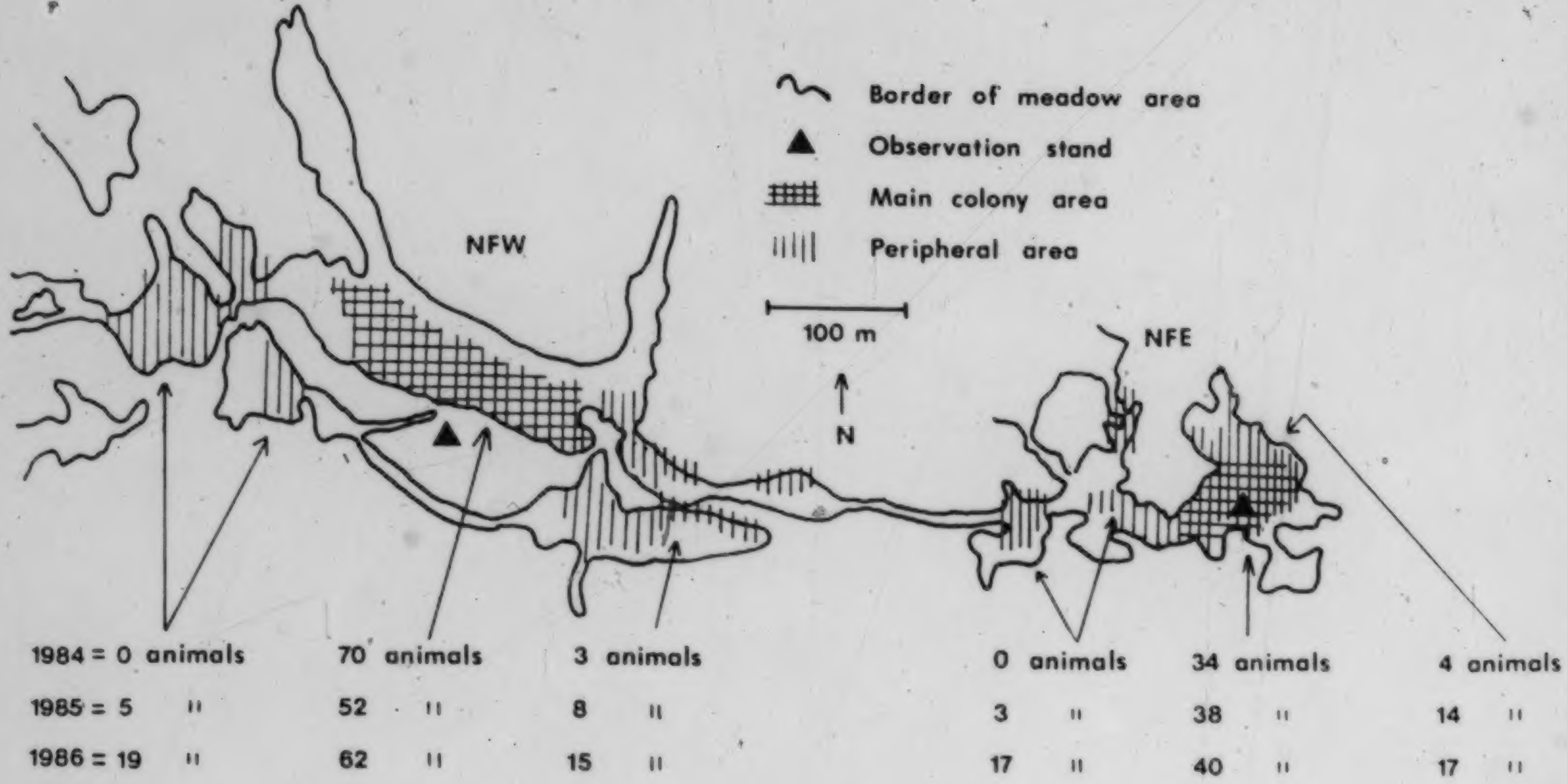
Hackett, D. 1987. Dispersal of Yearling Columbian Ground Squirrels. Unpubl. Ph.D thesis, Univ. AB, Edmonton.

Appendix 2. Distribution and number of adult and yearling Columbian ground squirrels on the main and peripheral portions of colonies NFW and NFE during 1984-1986.


Border of meadow area
Observation stand
Main colony area
Peripheral area
100 m
N
NFW
NFE
1984 = 0 animals
1985 = 5 "
1986 = 19 "
70 animals
52 "
62 "
3 animals
8 "
15 "
0 animals
3 "
17 "
34 animals
38 "
40 "
4 animals
14 "
17 "

Apppendix 3 Number of hours spent observing Columbian ground squirrels at three colonies (NFW, NFE, and RG) over the years 1984-1986.

	NFW			NFE			RG			
	1984	1985	1986	1984	1985	1986	1984	1985	1986	Total
Hours of observation in main colony area	159	204.25	126.5	135.25	221.5	132	71	223.5	147.25	1420.25
Hours of observation in peripheral areas	14	157.5	81.25	-	53.75	22	-	-	-	328.5
Number of observation days	64	95	64	65	81	54	33	83	60	599
Calander dates	May 7 to Aug. 9	April 22 to Aug. 6	April 8 to July 5	May 4 to Aug. 9	April 22 to Aug. 4	April 17 to July 18	May 18 to Aug. 7	April 24 to Aug. 6	April 15 to July 7	-

Appendix 4. An Improved Method of Sampling and Calculating Interaction Rates for Ground Squirrels

Rates at which ground squirrels interact have been calculated as the number of interactions per animal above ground per unit time (Michener 1980). An underlying assumption in such calculations is that all members of the "social group" being studied (eg. litter, harem, foraging group, colony) are continuously present and available to interact throughout the observation period. This assumption is known to be false for ground squirrels. For instance, Michener (1980) reported that, in a population of Richardson's ground squirrels (*Spermophilus richardsonii*), normally only 60% of individuals known to be present in the specific area were sighted above ground during any 12-minute period. In my studies of dispersal in Columbian ground squirrels (*S. columbianus*), I seldom observed both the mother and all of her yearling offspring simultaneously active above ground while the latter were still resident in the natal colony (Wiggett unpubl. data). Furthermore, individuals of many ground squirrel species occupy home ranges within the colony that are separated in space. Thus, these individuals seldom or never co-occur in either time or space and hence have virtually no opportunity to interact. Interaction rates therefore should be calculated on the basis of spatial and temporal "availability" of animals and not on the basis of number of animals observed over time (Michener 1980).

Michener did incorporate a spatio-temporal "availability" component into her calculations of interaction rates. She calculated the interaction rate for pairs of squirrels as the number of interactions observed between the pair divided by the number of times the two animals co-occurred in time and space. Michener decided that individuals of a pair were "available" to interact if both members were simultaneously sighted within a scan (12 minute duration) and if the two animals had home ranges that overlapped by at least 5%.

Although Michener's criterion of overlap is appropriate, it is not very precise; there were probably many instances when the two squirrels of an "overlapping" pair were not in spatial and temporal synchrony. For instance, although both squirrels may have been sighted within the same 12-minute scan, one squirrel may have been active above ground for the first 4 minutes while the other was active during the last 3 minutes. Even if two squirrels were in temporal synchrony, they may not have been spatially close enough to be "aware" of each other. For example if two squirrels had adjacent home ranges that overlapped by 5% and each animal's home range approximated a circle of 30m diameter, then the likelihood that the two animals were always spatially "available" to interact was probably low (5% or less) given that at any one time they could have been a maximum of 55 m apart.

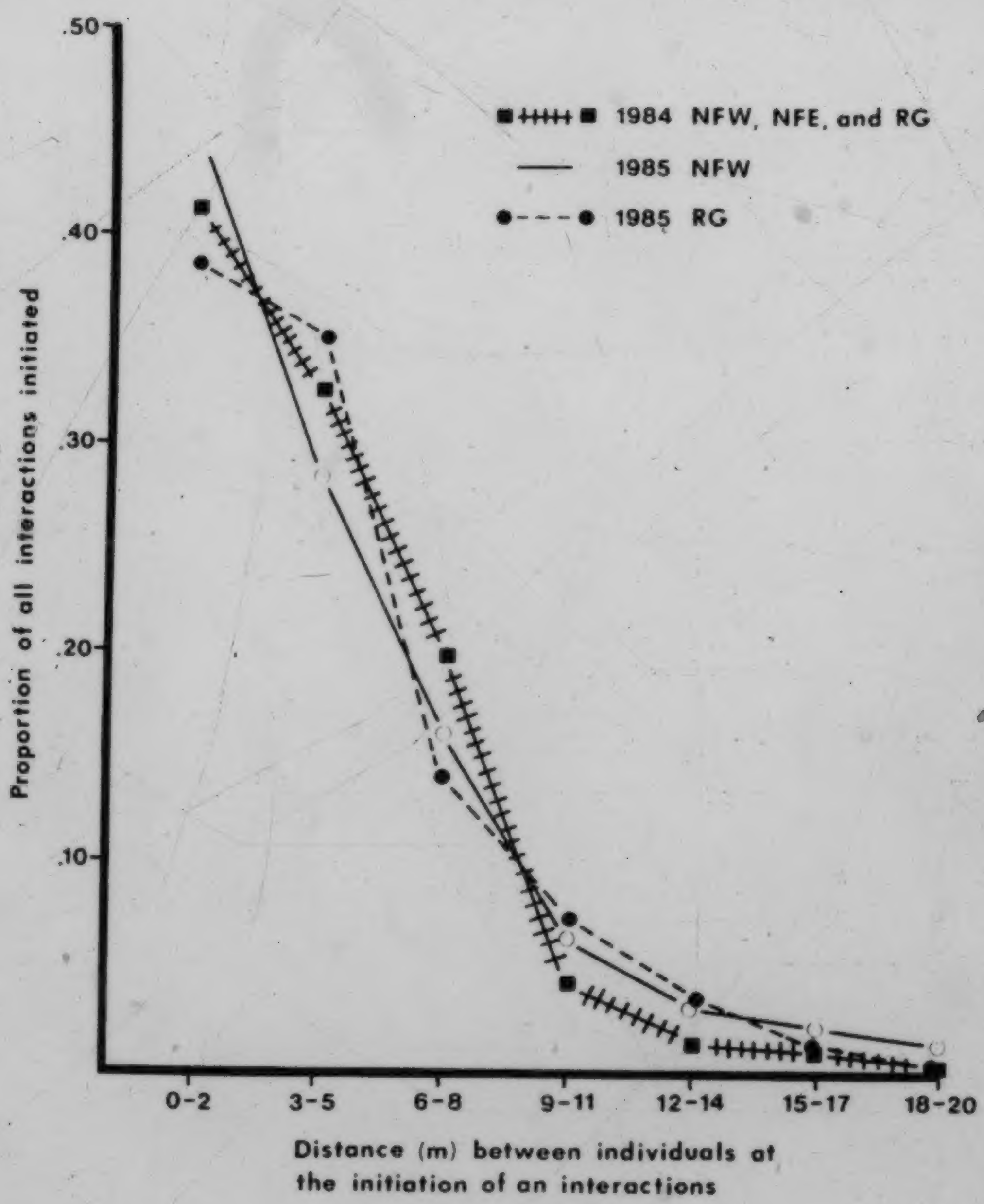
Obviously a more precise measure of spatio-temporal "availability" is desirable. The best solution would be to use only those instances when the two animals in question were known to be simultaneously active (temporally available) and were physically close enough that they were probably "aware" of each other and could interact if they so desired (spatially available). At what distance are two animals "aware" of each other? Determining this distance is difficult because it probably depends on motivational state of the squirrels and on environmental variables such as topography, vegetation, wind directions, etc. Nevertheless, an indirect way of assessing how far animals can be apart and still be considered to be spatially available to interact can be determined by sampling how far apart members of pairs of animals are when one or both individuals in a pair initiates an interaction. The distribution of these "initiation" distances would reveal a maximum "interaction distance" - that distance within which 95% of all interactions were initiated. Thus one could arbitrarily say that two animals were "available" to interact when they were simultaneously within the maximum interaction distance of each other. The interaction rate between a pair of animals would equal the total number of interactions observed divided by the total number of co-occurrances within the interaction "zone". Here I present data on initiation distances and determine the maximum interaction distance (zone) for Columbian ground squirrels on three study sites in southwestern Alberta. As well, I present a modified sampling regime suitable for collection of data under the constraints of the interaction zone (hereafter the spatio-temporal overlap) method of determining interaction rates. Finally, I compare my spatio-temporal overlap method of calculating interaction rates with Michener's scan-home range overlap method, and with the method based on number of interactions per animal per unit time.

Defining the Interaction Zone

Data on initiation distances were collected in 1984 and 1985 from colonies NFW, NFE, and RG (see Chapter 2 for descriptions of each area). All animals on these three areas were individually identifiable as they bore serially numbered eartags and unique body dyemarks (Chapter 2). Location of squirrels at any point in space within these colonies could be estimated to the nearest meter on the x and y axes of a grid laid over each study area (Chapters 2 and 3). In 71 instances during 1984 the distance in meters between two animals at the initiation of an interaction was known (all 3 colonies combined). In 1985 the distance between two animals of a pair at the initiation of an interaction was known in 222 and 359 instances at NFW and RG respectively.

Nearly three-fourths (73%) of all interactions were initiated when the two animals of an interacting pair were within 5 m of each other (Fig A4.1). Of all interactions, 96% were initiated at distances equal to or less than 11 m. The nearest whole number distance which most closely represented the theoretical 95% cutoff was 10 m (94.8% of all interactions were initiated when squirrels were within 10 m of each other). The similiarity between slope and pattern of the three lines on Fig A4.1 suggests that the distances that interactions were initiated were similar between colonies and between years. Based on this information, two squirrels were considered to be "available" to interact if they were sighted simultaneously within 10m of each other.

Fig A4.1. The proportion of interactions between individual Columbian ground squirrels that were initiated at various distances (m) at colonies NFW, NFE, and RG during 1984 and 1985.


.50
.40
.30
.20
.10
Proportion of all interactions initiated
■┼┼┼┼■ 1984 NFW, NFE, and RG
—— 1985 NFW
●- - -● 1985 RG
0-2
3-5
6-8
9-11
12-14
15-17
18-20
Distance (m) between individuals at the initiation of an interactions

Sampling for Spatio-Temporal Overlaps

Standard sampling procedures such as focal or instantaneous scan -sampling (Altmann 1974) do not provide adequate information to determine spatio-temporal overlap as outlined above. For example, standard focal sampling which involves recording details of activity and location of individuals over set lengths of time (Altmann 1974, Lehner 1979) provides no information on temporal or spatial relationships of the focal animal relative to its conspecifics. On the other hand, instantaneous scan sampling supposedly approximates a "photograph" of the relative location and activity of all animals in a group surveyed (Altmann 1974, Dunford 1977, Lehner 1979). In theory scan sampling could provide the type of information necessary to determine spatio-temporal overlap of individuals, but in practice recording the location and activity of numbers of individuals takes time and "instantaneous" scans may often be of relatively long duration (eg. 5-30 minutes - Dunford 1977). The distance recorded between two animals during instantaneous scan sampling may suggest that the two animals were in close proximity (eg. both were within 10 m of each other) when in reality the two animals may not have been close because their locations were recorded 5 minutes apart in the scan and both moved in the interim. Thus neither focal nor scan sampling are entirely appropriate for determining spatial and temporal overlap of conspecifics. More appropriate would be a sampling regime that provides information on the activity and location of individual animals relative to other animals within their "interaction zone" during a given instant in time. Such a sampling regime could be met by a combination of focal and scan sampling. A "focal-scan" sampling regime involves recording the location and activity of an individual "focal" animal while also noting the activity and location of all conspecifics which are within the maximum interaction distance (10 m) of the focal animal. In this manner focal-scan sampling would provide the information necessary to determine spatio-temporal overlap between "focal" animals and their nearby conspecifics.

I employed a "focal-scan" sampling regime during my studies of the dispersal behaviour of yearling Columbian ground squirrels (Chapter 4). Since I was primarily interested in yearling behaviour and spatial relations, I used focal-scan sampling on yearlings only; the behaviour of adults and juveniles was sampled using a regular scan sampling regime. At each colony "scans" were conducted on the main observation areas (Chapter 4 and Appendix 11) from left to right. For each yearling sighted; the time, identity, location, and behaviour of the yearling was recorded as was the identity, location, and behaviour of all other conspecifics that were within 10 m of the yearling in question. Each yearling was observed for 2 minutes and any interactions between the focal animal and the other "nearby" conspecifics were recorded. Thus, for each 2-minute "sighting" of a yearling a list could be made of all conspecifics that were "available" to interact with that yearling (eg. all conspecifics that were within 10 m of the focal yearling). Since the number of interactions between the focal yearling and its nearby conspecifics were recorded the interaction rate for any pair could be calculated as the total number of interactions between the pair divided by the number of times the two individuals were sighted within 10 m of each other.

Comparison Between the Three Methods of Calculating Interaction Rates

Data from six yearling son-mother pairs at NFE were used to calculate interaction rates for comparative purposes. The specifics of the 3 methods used to calculate interaction rates are outlined below.

Method 1 - This method is equivalent to the number of interactions per animal per unit time calculation discussed earlier. Specifically the interaction rate was calculated as the number of agonistic interactions (see Appendix 16 for details of behaviour types) between mother and son divided by the number of scans during which the son was sighted. Since scans were 15-minutes in duration the interaction rate per hour could easily be obtained by dividing by four.

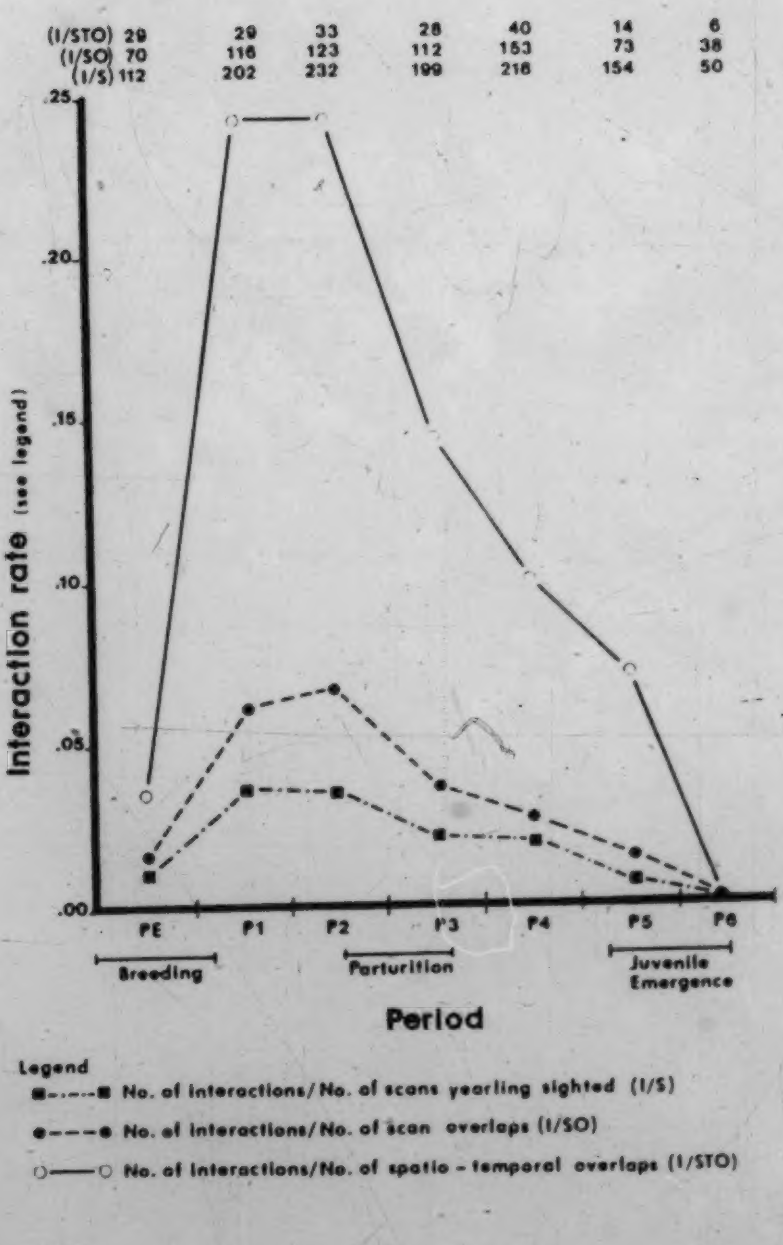
Method 2 - This method is essentially equivelant to Michener's (1980) "overlap" calculation of interaction rates. All six sons had home ranges that overlapped with that of their mothers' by at least 5% during Periods E to 6 (breeding, gestation, lactation, see Chapter 3 for details). The son and mother were assumed to be "available" to interact when both squirrels were sighted during the same 15 minute scan. Thus the interaction rate was calculated as the number of interactions between the pair divided by the total number of "scan-overlaps".

Method 3 - The mother and son were considered to be "available" to interact when the two occurred simultaneously within 10 m of each other. Interaction rates were calculated as the number of interactions between mother and son divided by the number of "spatial-temporal overlaps" between mother and son.

The interaction rate for all six mother-son pairs was calculated as the total number of interactions observed divided by the total number of scans, scan overlaps, and spatial-temporal overlaps observed between all the pairs. Interaction rates were calculated for all six pairs for each of the first seven 10-day periods (Periods E to 6) of the active season (see Chapter 3 for details). Only agonistic interactions between the mother and son were used in the calculations since they were the most numerous and unequivocal type of interaction (Chapter 6 and Appendix 17).

Both the scan and scan-overlap method of determining interaction rates suggested that agonistic interactions between mother and yearling son were relatively rare (Fig A4.2). On average sons and mothers were seen to interact agonistically only 2.1% of the time that sons were known to be active above ground and 3.6% of the time that both the mother and son were sighted above ground during the same scan. By contrast, the spatio-temporal calculation of the agonistic interaction rate suggested that mother and sons interact fairly frequently - 14% of all spatial-temporal overlaps between the mother and son resulted in agonistic interactions.

Fig A4.2. Agonistic interaction rate over time for six pairs of Columbian ground squirrels (mothers and their yearling sons) at colony NFE during 1986.

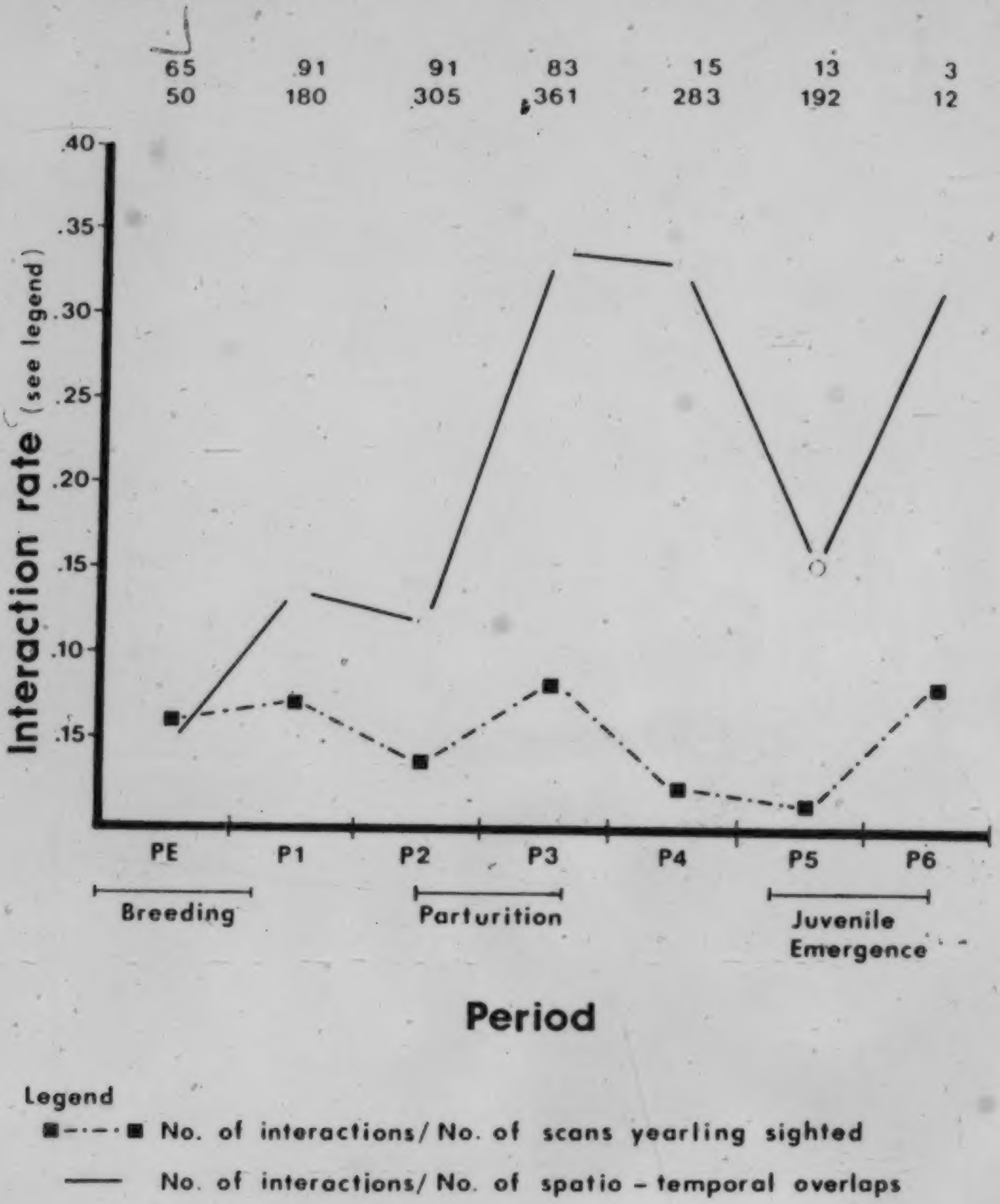


(I/STO) 29 29 33 28 40 14 6
(I/SO) 70 116 123 112 153 73 38
(I/S) 112 202 232 199 216 154 50
.25
.20
.15
.10
.05
.00
Interaction rate (see legend)
PE
P1
P2
P3
P4
P5
P6
Breeding
Parturition
Juvenile Emergence
Period
Legend
■-·-·-■ No. of interactions/No. of scans yearling sighted (I/S)
●- - -● No. of interactions/No. of scan overlaps (I/SO)
○——○ No. of interactions/No. of spatio - temporal overlaps (I/STO)

The spatio-temporal ovelap calculation probably provides the most "realistic" measure of interaction rate since it considers only individuals that are known to be spatially and temporally available to interact. In this case, both the mother and son were known to be simultaneously active above-ground at the same instant in time and as well were spatially near enough to one another to be within a biologically defined "interaction zone". Michener's method assumes overlap based on arbitrary measures of space (home range) and time (scans). Michener's scan-home range overlap method, although decidedly better than calculations based solely on the amount of time individuals were observed above-ground, is nevertheless not as meaningful biologically as the spatial-temporal overlap method presented here.

Although each of the three interaction rate calculations suggested different absolute levels of agonistic interaction, the pattern of interactions among the 3 methods was remarkedly similar (Fig. A4.2). In all 3 cases interaction rates peaked during Periods 1 and 2 and thereafter gradually declined to zero in Period 6. The similarity in pattern between the 3 interaction rates was not entirely surprising since one would expect that as the absolute number of scans within which a yearling was sighted increased, so too would the absolute number of scan-overlap and spatial-temporal overlap sightings increase. In other words, the number of scans, scan overlaps, and spatial-temporal overlaps were probably positively co-correlated (compare sample sizes for each method during each of the 7 time periods - Fig. A4.2). Nevertheless, such a co-correlation did not always exist. For example, Fig. A4.3 shows the pattern of agonistic interaction per scan and per spatial-temporal overlap between adult males and yearling males at colony RG during Periods E to 6 in 1986. The patterns of interaction rate between the two methods shown in Fig. A4.3 are not as similar to each other as were the patterns in Fig. A4.2. Although yearling males and adult males often resided in the same areas during period 3 and 4 (Chapter 3) and although both were often seen above-ground simultaneously, the frequency of agonism per scan observed was low (Fig. A4.3). On the other hand, during

Fig A4.3 Agonistic interaction rate over time for Columbian ground squirrels (adult males toward yearling males) at colony RG during 1986.


65 91 91 83 15 13 3
50 180 305 361 283 192 12
Interaction rate (see legend)
.40
.35
.30
.25
.20
.15
.10
.15
PE
P1
P2
P3
P4
P5
P6
Breeding
Parturition
Juvenile Emergence
Period
Legend
■-·-·■ No. of interactions/ No. of scans yearling sighted
—— No. of interactions/ No. of spatio – temporal overlaps

this same time period the spatio-temporal interaction rate was relatively much higher because the absolute number of spatio-temporal overlaps between adult and yearling males was low relative to the numbers of interactions seen. Thus this was a case in which there was no consistent relationship between the absolute number of scans observed and the absolute number of spatio-temporal overlaps observed (again compare sample sizes for each period).

In conclusion, both the absolute frequency and pattern of interaction may vary depending on the method used to calculate the interaction rate. Rates calculated on the basis of time spent observing (eg. number of scans) or on time spent by animals in presumed overlap (as in Michener's 1980 calculation) are inadequate for determining interaction rates because neither realistically measures "availability" to interact. The spatio-temporal overlap method of calculating interaction rates is the best alternative because both temporal and spatial coincidence of animals is known, not assumed, and spatial proximity has been defined "biologically" rather than arbitrarily.

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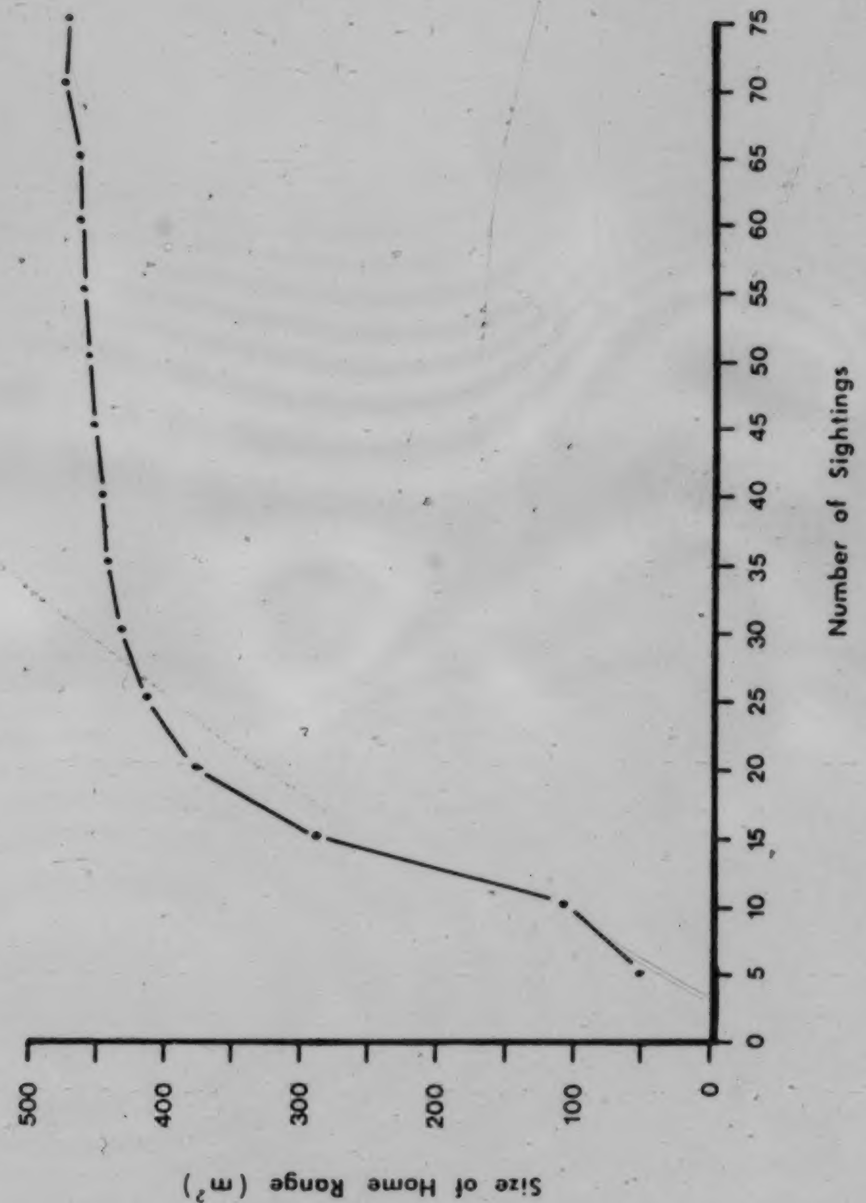
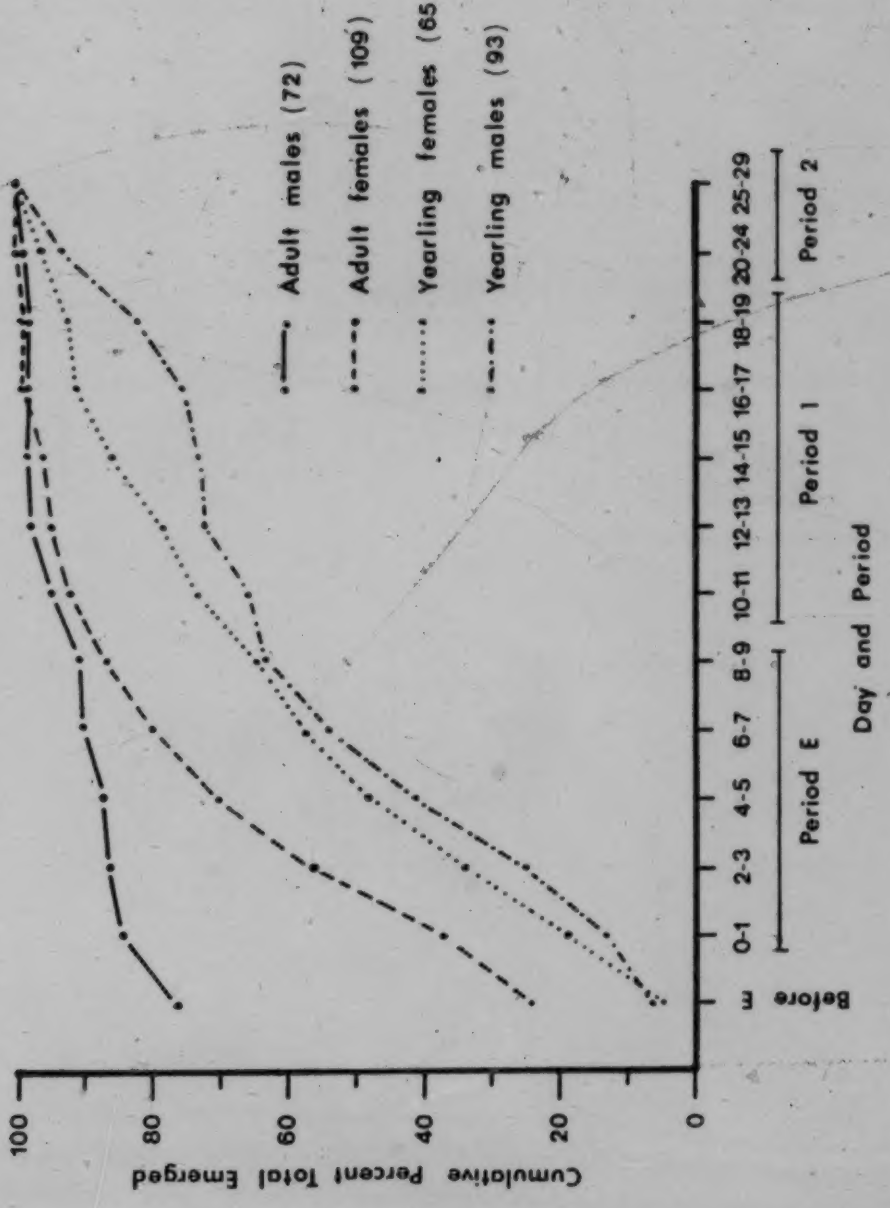
Appendix 5. Mean size of the home ranges of 12 adult female Columbian ground squirrels relative to the number of sightings for each female. Data are from colonies NFW, NFE, and RG (4, 3 and 5 animals respectively) that had a minimum of 75 sightings each during Period 6, 1985. Home range size was calculated as minimum convex polygons (Chapter 3).


Size of Home Range (m^2)
0
100
200
300
400
500
Number of Sightings
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75

Appendix 6. Emergence schedule by sex and age for Columbian ground squirrels at three colonies (NFW, NFE, and RG) during 1985 and 1986 (all years and sites combined).


Cumulative Percent Total Emerged
100
80
60
40
20
0
Before E
0-1
2-3
4-5
6-7
8-9
10-11
12-13
14-15
16-17
18-19
20-24
25-29
Period E
Period 1
Period 2
Day and Period
Adult males (72)
Adult females (109)
Yearling females (65)
Yearling males (93)

Appendix 7 Average of the largest home range sizes (80% core area) of 11 10-day periods for all age and sex classes of Columbian ground squirrels at three colonies (NFW, NFE, and RG) for the years 1985 and 1986 combined.

Age/sex	Mean home range size (m^2)	Range (m^2)	N	Mean diameter (m)	Period
Adult male	1160.3	226-4878	34	38.0	2
Adult female	415.5	97-1264	73	23.0	6
Yearling male	702.4	57-2413	73	30.0	3
Yearling[1] female	492.1	49-1854	38	25.0	3
Juvenile males	723.5	102-1258	85	30.4	8
Juvenile females	523.9	75-1158	57	25.8	8

[1] Excludes females that bred.

Appendix 8 Demographic characteristics of Columbian ground squirrels at three colonies (NFW, NFE, and RG) from 1984-1986.

	NFW			NFE			RG		
	1984	1985	1986[2]	1984	1985	1986[2]	1984	1985	1986[2]
Adults									
females	20	27	29^{-4}	14	20	29^{-5+2}	8	10	12^{-3}
males	5	11	20^{+2}	4	7	15^{-12}	5	6	7^{-5}
Yearlings									
females[1]	23^{1L}	11	18^{13B}_{9L}	12^{1L}	13	9^{3B}_{2L}	4	5	12^{11B}_{9L}
males	25	16	27	9	17	18	7	8	15
Spring population	73	65	94(92)[3]	39	57	71(56)[3]	24	29	46(38)[3]
Juveniles									
females	14	30	-	17	15	-	13	17	-
males	23	41	-	26	31	-	16	16	-
Immigrants									
females	2	3	1	2	3	0	0	0	0
males	2	8	3	5	2	6	3	3	4
Recruitement	41	82	-	50	51	-	32	36	-
Grand total	114	147	-	89	108	-	56	65	-

[1] B = number that bred and showed evidence of lactation, L = number than brought litters above-ground

[2] Number that emerged from hibernation, - = number of removals, + = number of successful introductions

[3] Spring population = number emerged (number of residents after removals and introductions)

Appendix 9 Meadow size, area used by and density of Columbian ground squirrels at colonies NFW, NFE, and RG from 1984 to 1986.

Colony/Year	Total meadow area (ha)	Total area (ha) used by squirrels	Spring population	Density animals/ha	Area (ha) and density (animals/ha) of: Main proportion of colony[1]	Peripheral areas
NFW 1984	5.1	1.34	73	54.5	1.24 (56.5)	0.10 (30.0)
1985	5.1	1.90	65	34.2	1.19 (43.7)	0.71 (18.3)
1986	5.1	3.47	94 (92)[2]	27.1	1.53 (39.9)	1.94 (18.0)
NFE 1984	2.5	0.77	39	50.6	-	-
1985	2.5	1.03	57	55.3	-	-
1986	2.5	1.30	71 (56)[2]	54.6 (43.1)	1.16 (58.6)	0.14 (21.4)
RG 1984	1.6	0.80	24	30.0	-	-
1985	1.6	0.73	29	39.7	-	-
1986	1.6	1.27	46 (38)[2]	36.2 (29.9)	-	-

[1] For details on "main" and "peripheral" areas of NFW and NFE see Appendix 2. The "main" proportion of NFE for this appendix was considered to be the "main" area plus the adjacent and flanking "peripheral" areas shown in Appendix 2. The "peripheral" area was considered those two satellite areas on the western edge of NFE in Appendix 2.

[2] Population after transplantation and removals.

Appendix 10. Criteria Used to Indicate Site of Hibernation for Individual Columbian Ground Squirrels.

Individual Columbian ground squirrels (*Spermophilus columbianus*) apparently dig an exit burrow from their hibernation chamber sometime before immergence into hibernation (Shaw 1925, Paul Young, person. comm.). At the time of immergence the exit burrow is incomplete, usually 5 to 20 cm of topsoil remains to be burrowed through upon emergence the following spring (Shaw 1925, P. Young person. comm.). The presence of a lethargic squirrel around a newly opened "exit" burrow is indicative of a newly emerged animal (P. Young person. comm.). As well, newly emerged animals characteristically have large white flakes of skin on the pelage (Murie and Harris 1982).

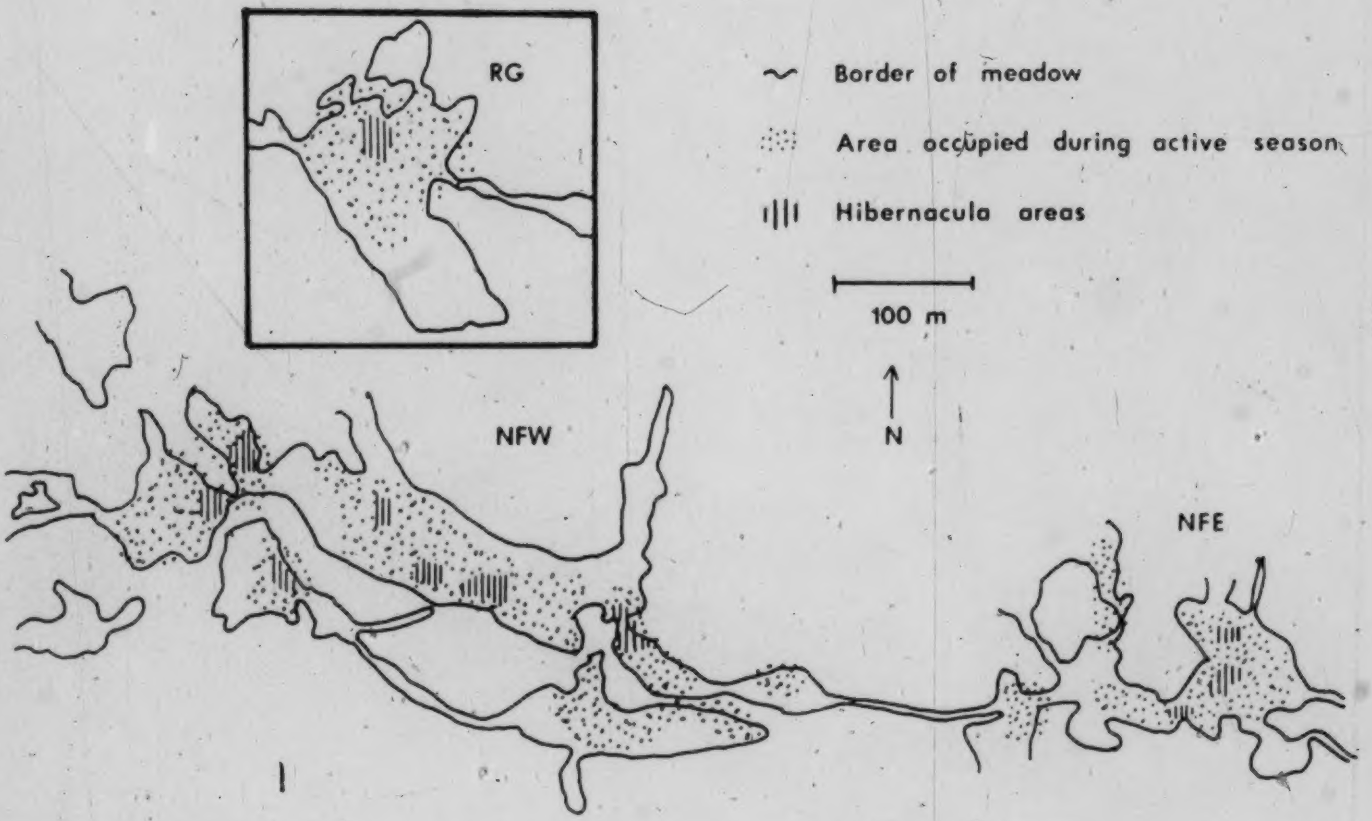
During the springs of 1985 and 1986 each of 3 study areas (NFW, NFE and RG) were scanned for newly-emerged squirrels. Upon seeing a squirrel not previously recorded as being active, the animal was captured , its pelage was examined as was the condition of the burrow from which it had emerged. If the animal was deemed to have just emerged, then the location of its exit burrow was recorded and this location was plotted on a map of the study area. The distribution of all exit burrows within the colonies studied indicated that within each colony exit burrows were highly concentrated in one or several "common" areas. For all animals for which the location at emergence was known, 222 of 249 (89%) emerged from within one of the "common" areas illustrated in Fig. A10.1. There was no evidence to suggest that individual Columbian ground squirrels shared hibernating chambers (Shaw 1925, P. Young person. comm.). I suspect squirrels using common hibernating areas were not sharing hibernacula *per se* but rather hibernacula used by different individuals were scattered within the "common" areas. The causes and consequences of clumped concentrations of hibernacula within colonies of ground squirrels is explored in Chapter 3.

Literature cited

Shaw, W 1925. The hibernation of the Columbian ground squirrel. Can. Field-Nat. 39:56-61, 79-82.

Murie, J.O., and M.A. Harris. 1982. Annual variation of spring emergence and breeding in Columbian ground squirrels (*Spermophilus columbianus*). J. Mamm. 63:431-439.

Fig. A10.1. Location of "common" areas of hibernacula at three colonies of Columbian ground squirrels (NFW, NFE, and RG) during 1985 and 1986.


RG
Border of meadow
Area occupied during active season
Hibernacula areas
100 m
N
NFW
NFE

Appendix 11 Mean size of home ranges of adult male Columbian ground squirrels during Periods 1-5. Data are combined from colonies NFW, NFE, and RG and years 1985 and 1986.

Period	1	2	3	4	5
Size (ha)	1015.2	1160.3	980.4	821.9	784.6
Range	(180-4601)	(226-4878)	(335-2570)	(323-1870)	(307-1526)
N	34	34	34	34	34

Appendix 12. Relinquishment of the Nest Site to Daughters by Adult Female Columbian Ground Squirrels.

Four adult females, two at NFW and two at NFE, apparently relinquished the maternal home range to their reproductively active yearling daughters in 1986. Squirrel A resided with two yearling daughters on the same home range that the mother had occupied the previous year. One of A's daughters showed signs of breeding (swollen and open vulva) and lactation (enlarged nipples). The other daughter did not breed. Female A moved and eventually established on a new home range approximately 3 to 5 days before giving birth. Female A shifted its activity centre by approximately 150 m from its previous activity centre and eventually raised a litter of 4 on this new home range as did its daughter (a litter of 3) on the old maternal home range.

Female B at NFW moved approximately 325 m to a new home range 4 to 6 days before giving birth. B's only offspring, a yearling female, showed signs of breeding and lactation and defended a nest burrow within its mother's former home range but the daughter was unsuccessful in bringing a litter above ground. B successfully brought 2 young above ground in the new home range.

At NFE two 3-year-old females that shifted their home ranges each had a yearling daughter that eventually brought a litter above ground in the areas where their mothers had previously resided. The mothers moved approximately 86 and 125 m from their former home ranges and settled in peripheral locations where no other squirrels had lived. Both of these adults eventually brought a litter above ground and both left their original home range just before giving birth (ca. 5 to 10 days in each case).

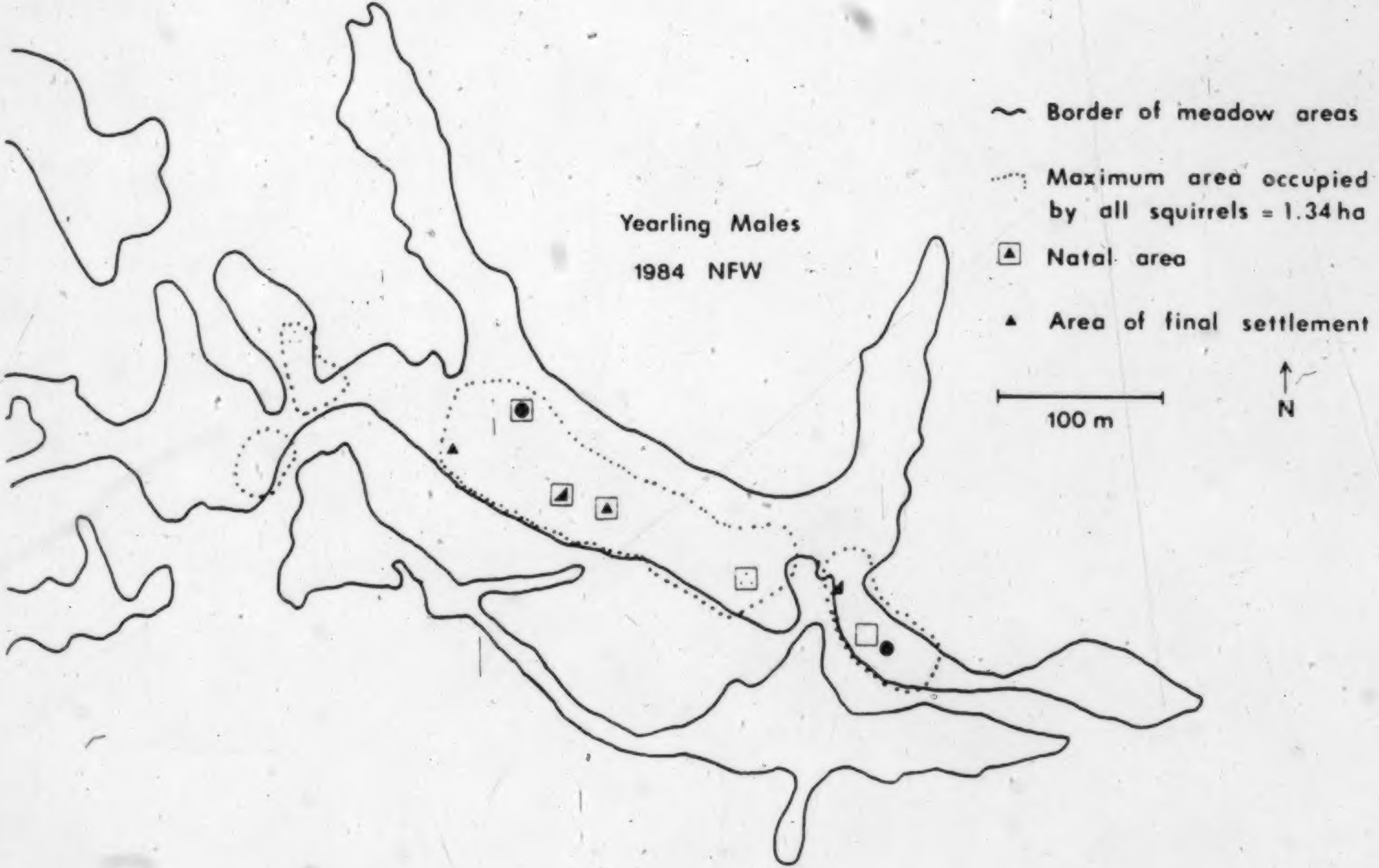
The only adult females that shifted their activity centres by greater than one home range diameter (40 m) after Period 1 were these four females, all of which had reproductively active daughters present (Chapter 3). All four adult females shifted their centre of activity just *before* giving birth which suggests that these females had given up their former maternal nest site in favour of the new area. Finally, all of the reproductively active daughters involved ultimately used their old natal sites. Of the four yearling females involved, all but one were successful in bringing a litter above ground.

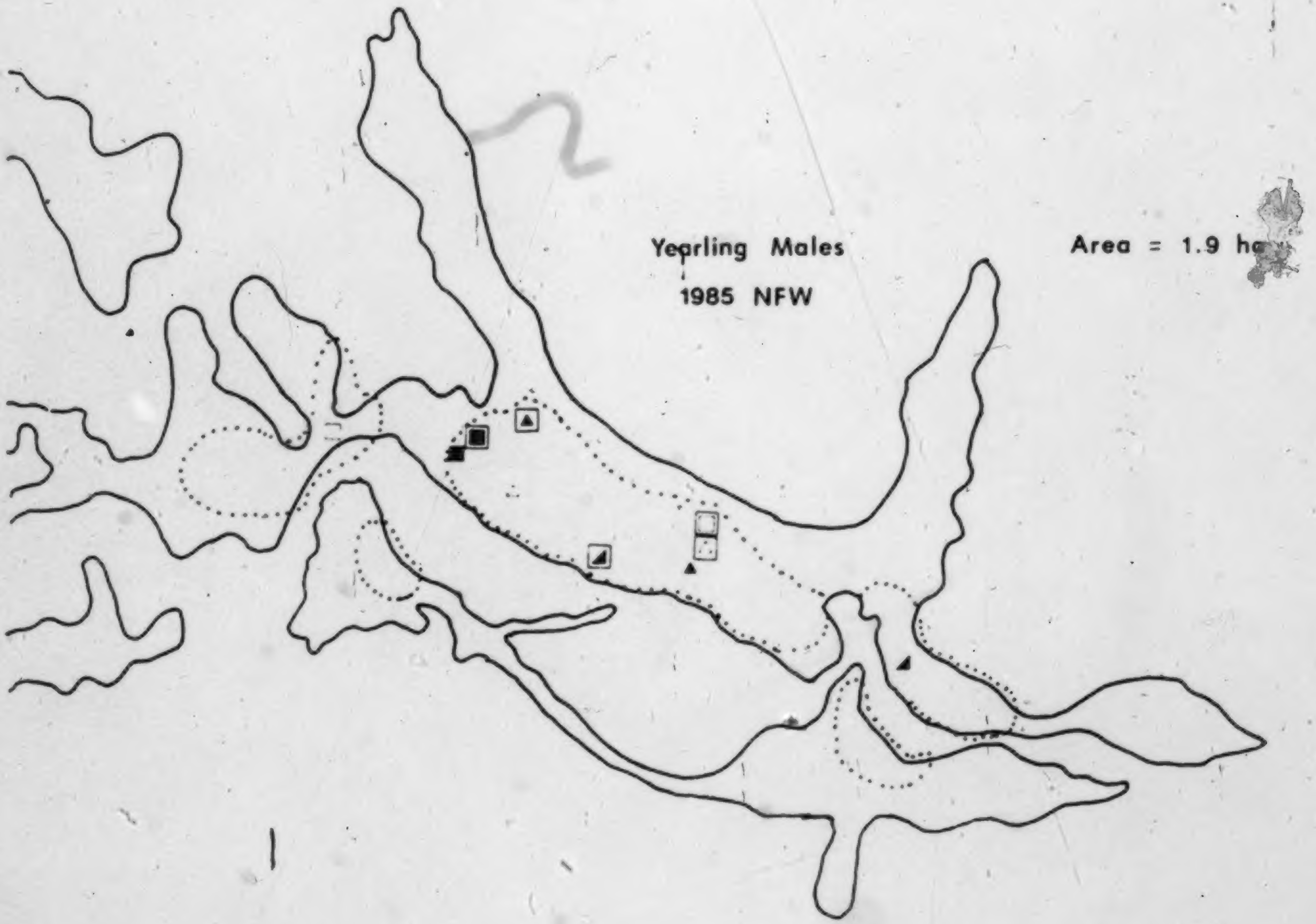
The evidence presented here suggests that, in some cases, adult females relinquish their nest site to their reproductively active daughters. Harris and Murie (1982) provided further evidence for the inheritance of nest sites among female Columbian ground squirrels and, as well, discussed the evolutionary consequences of such behaviour.

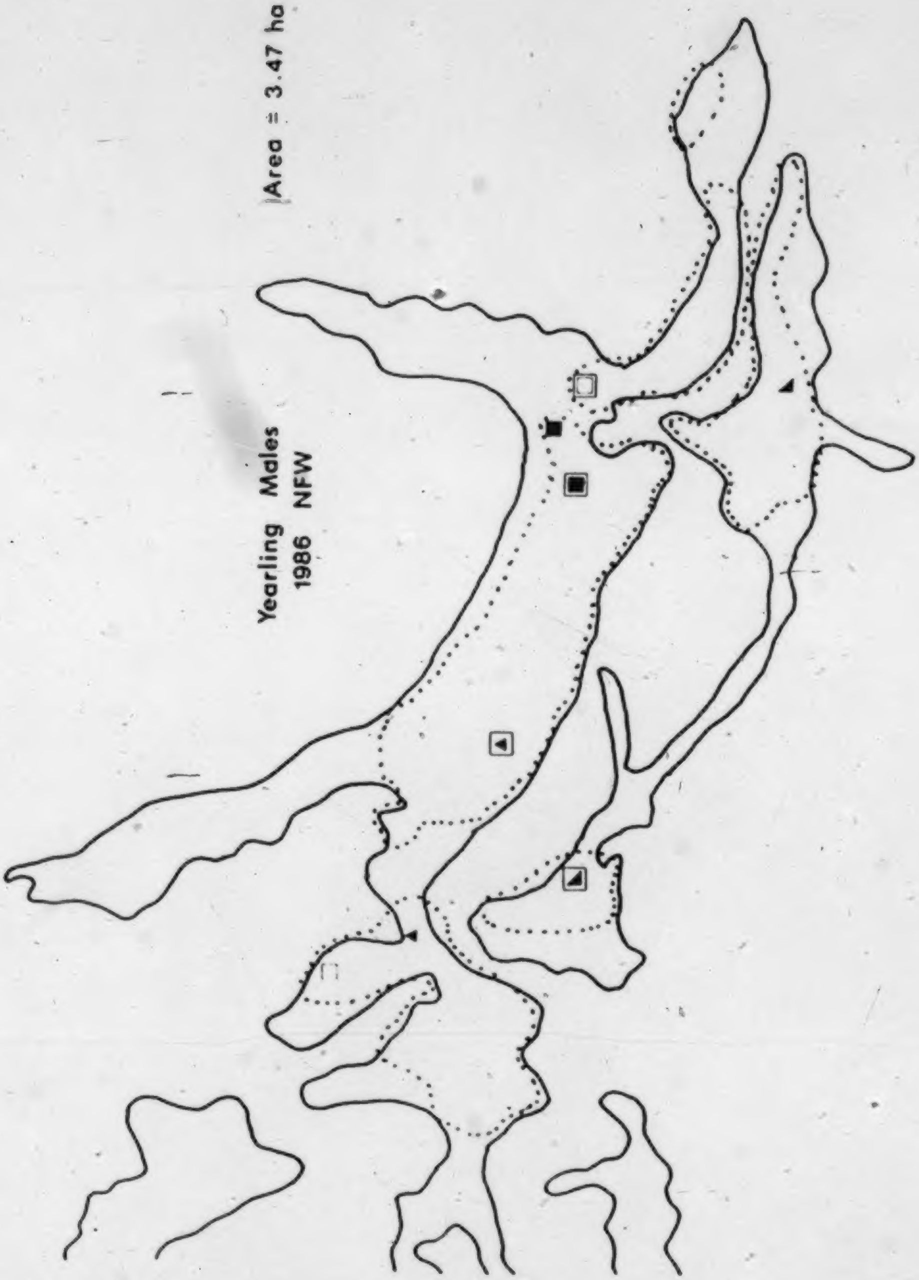
Literature cited

Harris, M. A., and J. O. Murie. 1982. Inheritance of nest sites in female Columbian ground squirrels. Behav. Ecol. 15:97-102.

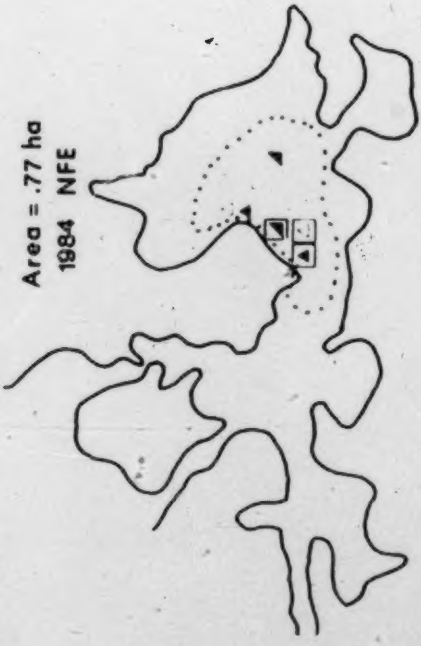
Appendix 13. Natal area of Columbian ground squirrels and site of final settlement for yearling male nondispersers and intracolony dispersers at NFW, NFE, and RG (1984-1986)


Yearling Males
1984 NFW
Border of meadow areas
Maximum area occupied by all squirrels = 1.34 ha
Natal area
Area of final settlement
100 m
N

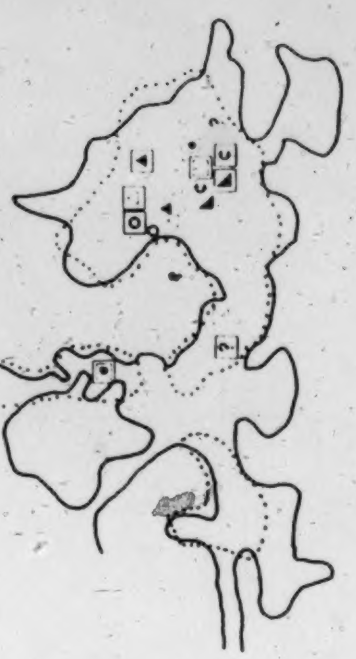

Yearling Males
1985 NFW
Area = 1.9 ha



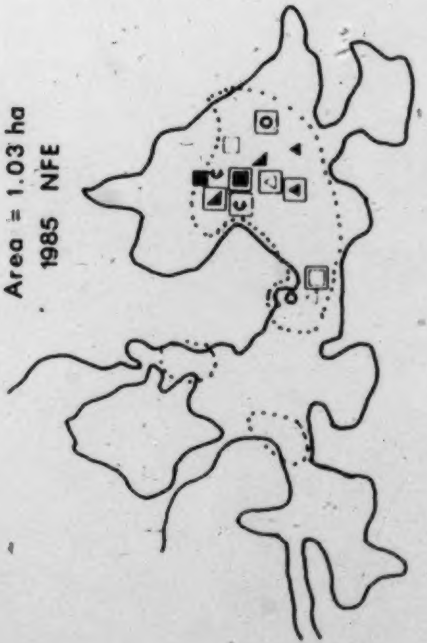
Yearling Males
1986 NFW



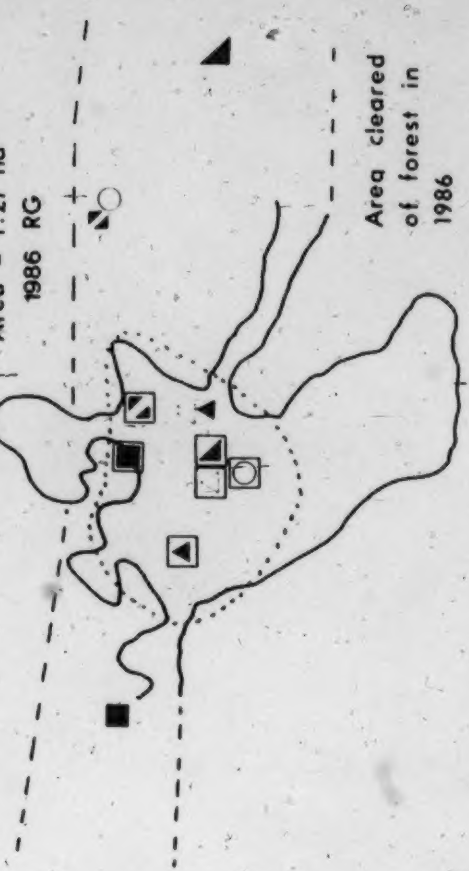
Area = .77 ha
1984 NFE



Area = 1.30 ha
1986 NFE



Area = 1.03 ha
1985 NFE



Area = 1.27 ha
1986 RG

Area cleared
of forest in
1986

Appendix 14. The Fate of Removed and Transferred Adult Squirrels

In 1986, 18 adult male and 11 adult female Columbian ground squirrels were removed from colonies NFW, NFE, and RG (see Fig 2.1 Chapter 2). These removals were undertaken as part of an experiment designed to test how yearling dispersal was affected by the presence or absence of mothers and/or siblings and the adult sex ratio (Chapter 6). As an alternative to sacrificing animals, those animals that were removed were transplanted into different colonies elsewhere. Animals to be removed were trapped as soon as possible after initial emergence from hibernation. Upon capture the animals were taken to either a studied or unstudied colony elsewhere where they were released (usually near the centre of the colony). All releases took place between April 10 and 29 coinciding roughly with the prebreeding and breeding periods of the squirrels.

In total 21 adults (13 male and 8 female) were removed and transferred into unstudied populations. Except for one individual, the fate of these squirrels remains unknown because the release areas were not subsequently trapped. One female that was released on the western edge of HM on 27 April 1986 was subsequently sighted at colony AA on the 12 July 1986 (see Fig 2.1, Chapter 2 for location of colonies). This female was recruited into that population and subsequently was successful in bringing a litter of three above ground in 1987.

Eight adults (5 males, 3 females) were introduced into colonies NFW (4 males), NFE (3 females), and GC (1 male). Two of the four males introduced onto NFW (from NFE) eventually established themselves within that population. Both ultimately settled on the periphery of the "main" study area at NFW (Appendix 2, one on the eastern edge, one on the western edge). The third male returned to NFE after spending 3 days on the main colony area of NFW. This male was born at NFW and had dispersed to NFE as a yearling in 1984. The fourth male was never resighted after it was released at NFW. The one male released at GC remained there and became a dominant territorial male in 1987.

All three females transferred were taken from NFW and released at NFE after they were estimated to have bred (see Chapter 2 for criteria). All three females eventually established "territories" (*sensu* Festa-Bianchet and Boag 1982) in peripheral areas that were seldom used by other resident squirrels. One of these females disappeared (died or dispersed) approximately 2.5 weeks after its release. The other two females each raised a litter successfully in 1986 and remained at NFE as permanent residents. Thus of the eight transfers into studied colonies, six were successful as the squirrels took up residency in the colony to which they were transferred. These results suggest that squirrels will remain and settle in colonies without need of the elaborate establishment techniques that seemed necessary to establish ground squirrels into empty habitat (Wiggett and Boag 1986). Whether or not squirrels will establish in meadows devoid of conspecifics but where vacant burrow systems exist remains to be tested.

Literature cited

Festa-Bianchet, M., and D.A. Boag. 1982. Territoriality in adult female Columbian ground squirrels. Can. J. Zool. 60:1060-1066.

Wiggett, D.R., and D.A. Boag. 1986. Establishing colonies of squirrels during their active season. Wildlife Soc. Bull. 14:288-290.

Appendix 15 The dispersal status of yearling female Columbian ground squirrels that bred and/or lactated at six C-1 colonies in southwesern Alberta.

Colony[1]	Years studied	Minimum number known to have bred[2]	Number bringing litters above-ground	Number of intracolony dispersers	Number of intercolony dispersers
NFW	1984-1986	14	10	0	0
NFE	1984-1986	4	3	0	0
RG	1984-1986	11	9	0	0
DC	1979-1986	15	15	-	0
AA	1984-1987	14	14	-	0
AB	1984-1987	2	2	-	0

[1] See Chapter 2, Fig. 2.1 and Table 2.1 for description of colony type and its location

[2] Based on condition of vulva and/or presence of copulatory plugs

Appendix 16. Social and Non-social Behaviours Sampled in Observations of Columbian Ground Squirrels

Non-social Behaviours (adapted from Dunford 1977, Holekamp 1983)

DUST BATHING - rolling or sliding on belly in dirt.

DIGGING - digging with front feet not followed by dust bathing.

FEEDING/EATING - any posture in which the jaws are moving, incudes foraging, walking or standing in any posture with the jaws moving or the forefeet manipulating food.

GROOMING/COMFORT - mouthing own fur; rubbing on fur with front feet; scratching, stretching, or yawning (for details see Steiner 1973).

LOCOMOTION - walking, running, trotting, nothing in the mouth, head up.

LYING - in prone posture, not engaged in any other activity; head held either above or on the substrate, jaws not moving.

COLLECT/CARRY NEST MATERIAL - nest material (dried grass, rootlets) in mouth, either collecting or running with it to burrow.

POSTING - remaining motionless in an upright "vertical" or "vertical stretch" position as described by Betts (1976).

SITTING - remaining motionless in "upright slouch" positions or on all fours as described by Betts (1976 - Fig 1g, h, and i:655).

SCENT MARKING - any scent marking behaviour described by Steiner (1974) that does not involve another animal or "dust-bathing" behaviour (see Figs. 1-5 in Steiner 1974).

CLIMBING - moving upwards on tree stumps, posts, bushes, etc.

NOSE TO SUBSTRATE - nose directed towards ground, jaws not moving, neither foraging nor scent marking; animal appears to be smelling the substrate.

Social Behaviours Sampled (adapted from Holekamp 1983)

Recognitive Behaviours - brief contact involving nose, mouth, and/or body.

NOSE TO NOSE - two animals touch noses; may be extended into "kissing" (see Steiner 1970b and Betts 1976).

NOSE TO BODY - the nose of one animal contacts the body of the other.

NOSE TO ANUS - the nose of one animal contacts the anogenital region of the other (see "inguinal nosing", Betts 1976).

Cohesive Behaviours - prolonged physical contact or close proximity without involuntary "forced" displacement of one animal by another.

SOCIAL GROOMING - grooming or licking of one animal by another (see Steiner 1970b, 1973, and Betts 1976 on "allogrooming").

SIDE BY SIDE - sitting or lying in physical contact with one or more conspecifics.

PLAY FIGHTING - wrestling or grappling without injury (see Steiner 1971 and Waterman 1986.

FOLLOWING - one animal follows another in an apparent attempt to maintain physical proximity with it.

CLOSE - animals feeding or sitting within 0.5 m of each other for at least 5 seconds without subsequent displacement of one animal by the other.

Agonistic Behaviours - overt aggressiveness, threat, submission; involves the displacement of one animal by another.

THREAT - usually directed towards an approaching animal; characterized by an arched back, fluffed tail, and usually an open mouth.

CIRCLING - walk with heads and fanned tails directed towards each other in a decreasing spiral movement (see Fig. 3 in Betts 1976).

SPARRING - one or both animals strike out with the forepaws at the other individuals.

RUN AT - one animal runs towards the other resulting in the displacement of the sedentary animal.

LUNGE ATTACK - one animal pounces on another with the forefeet.

BALL FIGHT - grappling or wrestling usually with injurious bit and often accompanying vocalizations.

STANDOVER - one animal stands on or over top of the other animal.

SUBMISSION - animal rolls on back and exposes underparts to other animals (Steiner 1970, 1971).

Ambiguous Behaviours - behaviours for which the social context is not clear or is not known.

MOVE TOWARDS - one animal moves toward another but no interaction or displacement takes place.

RUN AT - one animal runs toward another but no interaction or reaction ensues.

FOLLOW INTO BURROW - one animal follows another into a burrow - since the outcome of the interaction (if any) takes place below ground, the behaviour remains ambiguous in context.

REBOUND - one animal runs or walks towards another but retreats just before or after contact.

RECOIL - intense and rapid withdrawal (ie. running) from an approaching animal.

Literature cited

Betts, B.J. 1976. Behavior in a population of Columbian ground squirrels (*Spermophilus columbianus columbianus*). Anim. Behav. 24:652-680.

Dunford, C. 1977. Social system of round-tailed ground squirrels. Anim. Behav. 25:885-906.

Holekamp, K.E. 1983. Proximal Mechanisms of Natal Dispersal in Belding's Ground Squirrels (*Spermophilus beldingi beldingi*). Unpubl. Ph.D. thesis, Univ. Calif. Berkeley.

Steiner, A.L. 1970a. Etude descriptive de quelques activites et comportements de base de

Spermophilus columbianus columbianus (Ord.). 1. Locomotion, soins de corps, alimentation, fouissage, curiosite et alarme, reproduction. Rev. Comp. Animal 4:3-21.

Steiner, A.L. 1970b. Etude descriptive de quelques activites et comportements de base de *Spermophilus columbianus columbianus* (Ord.). 2. Vie de groupe. Rev. Comp. Animal 4:22-42.

Steiner, A.L. 1971. Play activity of Columbian ground squirrels. Z. Tierpsychol. 28:247-261.

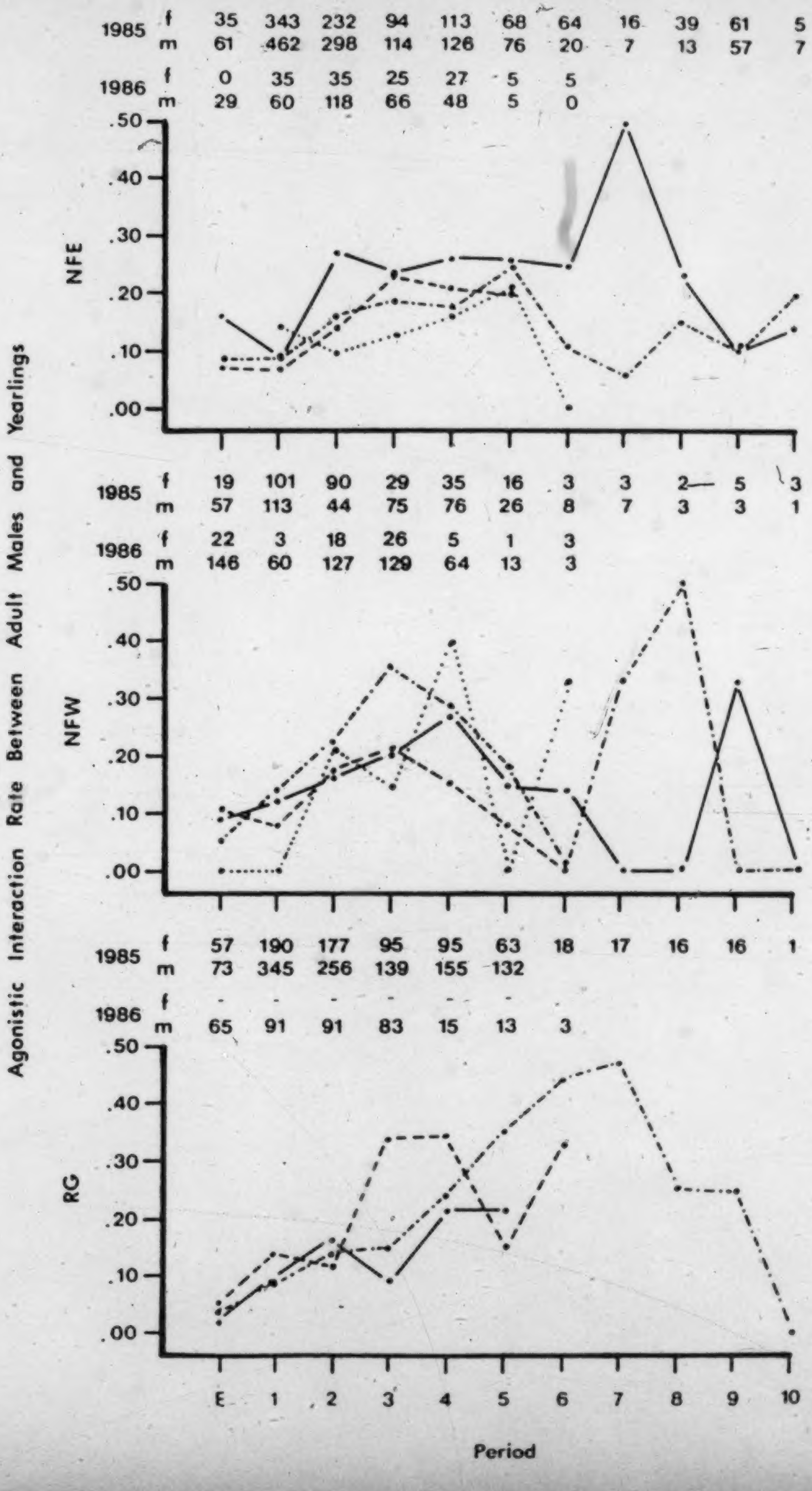
Steiner, A.L. 1973. Self- and allo-grooming behaviour in some ground squirrels (Sciuridae), a descriptive study. Can. J. Zool. 51:151-161.

Steiner, A.L. 1974. Body-rubbing, marking, and other scent-related behaviour in some ground squirrels (Sciuridae), a descriptive study. Can. J. Zool. 52:889-906.

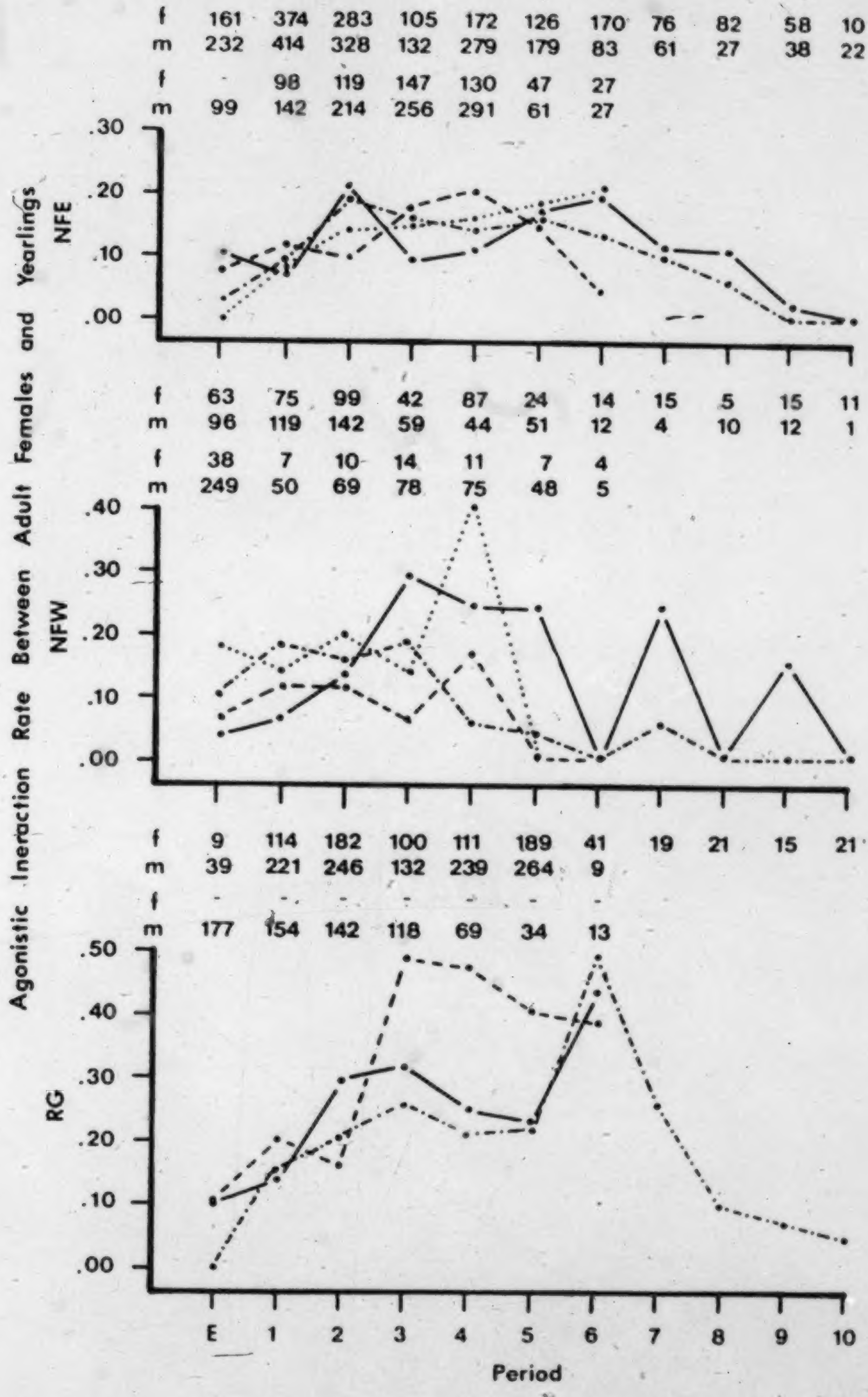
Appendix 17 Percent (number) of social interactions among Columbian ground squirrels that were agonistic, cohesive, recognitive, or ambiguous. Data are combined for colonies NFW, NFE, and RG and years 1985 and 1986. Includes all age and sex classes.

Agonistic	Cohesive		Recognitive	Ambiguous	Total
	Play	Other			
45% (3789)	20% (1692)	16% (1332)	5% (441)	14% (1193)	100% (8227)

Appendix 18a. Agonistic interaction rate between adult male and yearling Columbian ground squirrels at colonies NFW, NFE, and RG during 1985 and 1986. Sample sizes are given above each period. 1985 yearlings; •————• males, •—·—·—·—• females. 1986 yearlings; •— — — — —• males, •··········• females.


Agonistic Interaction Rate Between Adult Males and Yearlings
1985 f 35 343 232 94 113 68 64 16 39 61 5
m 61 462 298 114 126 76 20 7 13 57 7
1986 f 0 35 35 25 27 5 5
m 29 60 118 66 48 5 0
NFE
.50
.40
.30
.20
.10
.00
1985 f 19 101 90 29 35 16 3 3 2 5 3
m 57 113 44 75 76 26 8 7 3 3 1
1986 f 22 3 18 26 5 1 3
m 146 60 127 129 64 13 3
NFW
.50
.40
.30
.20
.10
.00
1985 f 57 190 177 95 95 63 18 17 16 16 1
m 73 345 256 139 155 132
1986 f - - - - - -
m 65 91 91 83 15 13 3
RG
.50
.40
.30
.20
.10
.00
E
1
2
3
4
5
6
7
8
9
10
Period

Appendix 18b. Agonistic interaction rate between adult female and yearling Columbian ground squirrels at colonies NFW, NFE, and RG during 1985 and 1986. For legend see Appendix 18a.


f 161 374 283 105 172 126 170 76 82 58 10
m 232 414 328 132 279 179 83 61 27 38 22
f - 98 119 147 130 47 27
m 99 142 214 256 291 61 27
.30
.20
.10
.00
NFE
f 63 75 99 42 87 24 14 15 5 15 11
m 96 119 142 59 44 51 12 4 10 12 1
f 38 7 10 14 11 7 4
m 249 50 69 78 75 48 5
.40
.30
.20
.10
.00
NFW
f 9 114 182 100 111 189 41 19 21 15 21
m 39 221 246 132 239 264 9
f - - - - - - -
m 177 154 142 118 69 34 13
.50
.40
.30
.20
.10
.00
RG
E 1 2 3 4 5 6 7 8 9 10
Period
Agonistic Ineraction Rate Between Adult Females and Yearlings